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OBSERVATIONS ON DIURNAL MIGRATION OF PLANKTON CRUSTACEANS IN LAKES SHIKOTSU, HOKKAIDO, AND TSUGARUJUNI, AOMORI, AND SOME EXPERIMENTS ON PHOTO- AND GEOTROPISM

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I. Introductory and Historical

Many planktonic animals, especially crustaceans, migrate up and down periodically during a day; this movement has attracted the attention of numerous investigators. General reviews on this problem have been written by Russell (1927b), Kikuchi (1930b, 1939), Clarke (1934c), Welch (1935, pp. 226-235) and Cushing (1951), which are very useful for workers following after them.

Many years ago Forel (1876) and Weismann (1877) made observations on the change of vertical distribution of plankton with respect to hours, seasons and weathers at Lake Leman and the Bondensee respectively. Ruttner (1905) worked at Plön on this subject. At lake Kizaki in Japan, Kikuchi (1927, 1930a) found that some copepods and cladocerans appear on the surface at night, while others migrate up to the surface only in the twilight of early morning and evening. He (1937) found by experiments that the vertical distribution of the most of cladocerans is closely correlated with the light intensity, but not with the water temperature. In the elaborate work of Worthington (1931) at the Lake of Lucerne, a fair display of diurnal vertical migration of cladoceran plankton was shown. Langford (1938) carried out observation on the diurnal changes in the distribution of the crustaceans of Lake Nippissing, Ontario, and came to the conclusion that light, modified by other environmental factors, is the most important causal factor involved, but that there are specific differences in response to these changing conditions. Coker and Hayes (1940) worked at Mountain Lake in Virginia, and found that the numbers of plankton crustaceans increase in the epilimnion at night; Grover and Coker (1940) gave a more detailed account of the movement of plankton in this lake. The author (Motoda and Ishida, 1950) has observed the vertical distribution of daphnids, copepods and mysids at Lake Abashiri, Hokkaido, throughout 24 hours.

In the salt-water lake, Lake Hiruga, Kikuchi (1930a) found that some copepods, cladocerans, chaetognaths and brachyuran zoea appeared abundantly at the time of sunset or a few hours after, but on the contrary, *Evadne* sp. was distributed on the surface in

daytime and migrated down to the depth at night.

Besides the above, investigators engaged in the work at sea have also contributed much to the present subject. Esterly (1911, 1912) observed the diurnal movement of copepods in San Diego region; Michael (1911, 1913) reported on chaetognaths. Russell investigated in the Plymouth area, England, and published numerous papers dealing with the vertical distribution of macroplankton (Russell, 1925, 1926a 1926b, 1926c, 1927a, 1928a, 1928b, 1928c, 1930, 1931a, 1931b, 1934). He (1926c) stated that various plankton animals are most frequently distributed in the optimum range of light intensity and they change the distribution according to the weather condition as well as to the time in a day. Farran (1926) observed in the Bay of Biscay that the copepod population from the surface to 100 fathoms approximately doubled during the night by an upward migration. Clarke (1933) gave the results of investigations in the Gulf of Maine, reporting that the diurnal migration of copepods has neat correlation with changes in submarine irradiation. He (1934a) found also the migration of copepods through a vertical distance as large as 120 metres in the deep water of the Gulf of Maine. The extreme instance of migratory habits in marine copepod was observed by him (1934b) at St. Georges Harbour in Bermuda Island. He found that *Calanopia americana* burrows into the mud of the bottom during midday. Welsh, Chase and Nunnemacher (1937), in the voyage of the "Atlantis" investigated the diurnal migration of abyssal plankton in Sargasso Sea, Atlantic. They indicated that the plankton animals do migration at a great depth passing through the layer of 400 metres. Later, Waterman, Nunnemacher, Chase and Clarke (1939) made an observation on the diurnal migration of deep-water plankton at a station in continental slope water of the western North Atlantic. According to them, all of the malacostracan crustaceans exhibit diurnal migrations 200 to possibly 600 metres in vertical extent. Johnson (1938) observed the vertical movement of a copepod, *Acartia tonsa*, at Passamaquoddy Bay, and also made a few laboratory experiments, finding that light is an important factor governing the diurnal movement. Bogorov's (1946) work in Polar Seas is very interesting in considering the relation between the light and diurnal movement. He mentioned that zooplankton in the Barents Sea under conditions of permanent day-light in summer performs no such regular up and down movement during a 24 hour period; *Calanus finmarchicus*, *Sagitta elegans* and other forms maintain an almost unchanged vertical distribution throughout the 24 hours. However, they manifest regular diurnal migration under conditions of alternating day and night in autumn, clearly aggregating in the upper 50 metre layer in the hours of darkness.

In Japan Shimomura (1948, 1950) carried out observations on the time variation of the constitution and quantity of plankton at a station in the North-west Pacific (39°N, 153°E). He stated that the plankton varied greatly with time even in such a high sea point. The author (Motoda and Sato, 1949) made a brief observation on the diurnal migration of marine zooplankton off Shiretoko, north-eastern Hokkaido, and classified the diurnal movement of plankton into three main types. Marumo and Kawarada (1951) and Kawarada (1952), investigating in Sagami Bay, reported that plankton volume fluctuated diurnally

corresponding to physical and chemical changes of water.

Recently Moore (1950) reported that such diurnal movement of plankton animals can be caught by means of echo-sounding. According to him, the diurnal movement of euphausiids in the deep water corresponds to the daily change of what are exhibited on bathygrams (records from echo-sounders); the'layer at which the sound waves are reflected is named the "Deep Scattering Layer".

In addition to the field observations referred to above, there have been many laboratory experiments on the tropism of the plankton animals aimed at a solution of the behaviour in the diurnal migration. The first investigators on this problem, Groom and Loeb (1890) stated that the larvae of barnacles move down because they are of negative tropism towards the intense daylight. Parker (1902), working on the copepod, *Labidocera aestiva*, also found that animals are positively phototropic to faint light, but negative to strong light. Rose (1925) obtained similar results with *Daphnia longispina* and some marine copepods and also Clarke (1930) with *Daphnia magna*. However, the results of experiments by Bolin (1929) with rotifers showed that they are always negatively phototropic in either strong or weak light. Johnson (1938) indicated after a few experiments that the copepod, *Acartia clausi*, is more attracted to weak light than to strong light. Kikuchi (1938) also by experiment learned that the phototropic sign of plankton crustaceans changes with the intensity of light; some are positively phototropic to weak light, but negative to strong light, and others are indifferent to weak light and become negative phototropic to very strong light. Furthermore, sudden change of intensity of light induces a temporary change of phototropic sign of animals.

Loeb (1894, 1908) always found the phototropic animals to be positive either to vertical or to horizontal light, but Bauer (1908, 1909) stated that the mysids react to only vertical light, and the light mainly comes from above in natural habitat. However, Foxon's (1940) experiments showed that the mysids react regularly to horizontal light, but when the lighting is from above they remain or move in any direction.

The phototropic sign of animals is also reversed by a change of temperature. Loeb (1893) first reported that the plankton crustaceans become phototropically positive by cooling and negative by warming. Esterly (1919) also mentioned that marine copepods, *Acartia tonsa* and *A. clausi*, become negative in the cold water having been removed from the surface of the sea, and that *Calanus finmarchicus* and *Metridia lucens* are strongly negative to any intensity of light at ordinary temperatures, but become strongly positive when brought into cooled water of 10°C or less. Rose (1925) stated that *Daphnia longispina* and some marine copepods change their phototropic sign with a change of temperature. *Daphnia longispina* studied by Kikuchi (1938) showed a slight tendency to a negative phototropism by sudden raising or lowering of the water temperature. However, *Acanthodiaptomus yamanacensis* was always positive in phototropism without regard to temperature.

A change in the concentration of salts or changes in the amount of dissolved gases or addition of some chemicals also induce the reversal of phototropic behaviours of animals in the water. Loeb (1893) learned that small animals become positive in phototropism when sodium chloride is added in sea water. Later, he (1904, 1906) found that copepods, daphnids and *Gammarus* react positively to light in the water containing comparatively large amount of carbon dioxide. He (1908) regarded that, among the external conditions, light, as well as the acidity and temperature of the surrounding water, is an important factor which affect the sign of phototropism. On the protozoan, *Paramaecium*, and echinoid larvae (*Diadema setosum*) Fox's (1925) experiments indicated that acid and alkali in the water also affect their phototropism. Rose (1925) indicated that the maximum sensitivity of plankton animals to light appears in the neutral water. Hardy and Paton's (1947) experiment, however, showed that the differences in pH value of the water within the range of 7.57-8.75 do not markedly affect the behaviour of *Calanus finmarchicus*. Clarke (1930) found that *Daphnia* advances to the light in normal condition, but it goes back without changing the direction of the body when strychnine is added into the water. Other experiments by Mori (1937, 1939) revealed that alcohol added into the culture medium does not change the phototropic sign of *Moina macrocopa*, but accelerates its behaviour.

Phototropism of animals is also affected by the amount of food on which they feed. According to the observation of Clarke (1930), phototropism of adult *Daphnia* is not remarkable in normal condition of nutrition, but it becomes strongly positive when the food is exhausted. Hardy and Paton (1947) made a few experiments to compare the vertical migratorial behaviour of *Calanus finmarchicus* which were well fed and those which had been starved, but the results were inconclusive.

Reversal of geotropic sign of plankton animals with the change of environmental conditions has also drawn the attention of investigators. Esterly (1907) found that females of *Cyclops albidus* which are positively geotropic in normal condition become negative when removed from strong light into darkness. However, they later regain positive geotropism after a while in darkness (Esterly, 1912). His further experiments (1917a, 1919) showed that marine copepods and chaetognath alter their geotropic sign with change of light conditions. The experiments of Harper (1907) on *Corethra* larvae, of Mcginnis (1911) on *Brachiopus*, of Dice (1914) on *Daphnia* and of Fox (1925) on *Paramaecium* and echinoid larvae proved the reversal of geotropism with change of light intensity. Kikuchi (1938) also experimented on the relation between geotropic sign of cladocerans and copepods and condition of light. Generally the increase of light intensity is said to produce a tendency to positive geotropism, while a decrease in light intensity results in a tendency to negative geotropism. Schallek (1943) found by experiments that *Acartia tonsa* only reacts to direct light, while in diffuse light it sinks passively under the influence of gravity.

The change of temperature of surrounding water induces the change of geotropic sign of animals. Experiments of Parker (1902), Dice (1914), Esterly (1919) and Kikuchi (1938)

showed a general tendency that high temperatures produce positive geotropism and low temperatures negative geotropism. These changes, however, are differently induced when the animals are either exposed to light or laid in darkness.

Hardy and Paton (1947), after experimenting with specially designed apparatus, suggested that *Calanus finmarchicus* would appear to have a sense of depth. The ascending and descending movement of *Calanus* seems directly correlated with the depths at which the experiments were made, and not to light intensity. However, whether the animal has "sense of depth" or not is still unknown. Later, Hardy and Bainbridge (1951a) carried out expriments on how the behaviour of crustacean plankton is influenced by the change of pressure. While no effect of pressure on the behaviour of *Calanus finmarchicus* was detected, striking results were obtained with larvae of zoea and megalopa stages of *Portunus* and *Carcinus* which showed upward movements when laid under the increasing pressure equivalent to depths of 10 and 20 metres.

It has been recognized from field observations as well as from laboratory experiments that close kinship of plankton animals is not responsible for any similarity of migratory behaviour. Various species are not equally affected by external factors which may stimulate and govern the migration. Consideration of this fact forces one to the presumption that specificity in behaviour of each species must be taken into account as Parker (1902) and also Esterly (1917a, 1919) insisted. It would be desirable to obtain the perfect features of diurnal vertical migration of various species under varying circumstances. Owing to the necessity for exceedingly painstaking laborious work, contributions in this field of study are mostly fragmental, and many facts are yet concealed unsolved.

The present investigation has been attempted to ascertain datailed features, as completely as possible, of the diurnal movements of each species of plankton crustaceans in Lake Shikotsu, Hokkaido. Since the preliminary observation at this lake was inaugurated in August, 1942, the observations in the field have been repeated in two successive years; viz., in summer of 1943, late spring, summer and autumn of 1944, stress having been laid particularly on the summer observations of 1944. To compare the migratory behaviour of plankton in this transparent Lake Shikotsu with that in turbid water, the author had an opportunity to make investigation at Koikuchinoike of Tsugarujuni Lake Group in Aomori Prefecture in July, 1943. The field observations were performed ten times in total covering different seasons, years and localities; the plankton hauls numbered eighty-four times in all. The sum total of intact sample vials came to four hundred and eighty-seven, exclusive of broken vials. In the laboratory brief experiments on the phototropic and geotropic behaviours of various species were carried out for consideration in relation to the relative depths of their vertical distribution in nature. These experiments were made in the laboratory at Sapporo and also in the Fish Hatchery at Lake Shikotsu in October, 1946, and July, 1948. The outbreak of hostilities made the research work pretty difficult in every aspect, and conditions were not improved after peace was recovered. Regrettably, on account of

many disadvantages the observations and experiments performed were not satisfactory, but the main results obtained were felt to be sufficiently useful to record.

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III. Hydrography of Lakes Investigated

The field observations on the diurnal movement of plankton were carried out mainly at Lake Shikotsu in Hokkaido, but an observation was also performed at Koikuchinoike of Tsugarujuni Lake Group in Aomori Prefecture. These two lakes show an excellent contrast with each other in area, depth, transparency of water, productivity and so forth. The former lake is typically oligotrophic, while the latter belongs to the eutrophic type. It is expected that the features of vertical migration of plankton in the two lakes would show some divergence according to the environmental differences. This is the chief reason why these two lakes were employed in the present research.

Lake Shikotsu

This lake has been investigated by Handa in 1915 (unpublished), Nagamine in 1922 (unpublished), Tanakadate (1925), Sawa (=Kondo) in 1926 (unpublished), Yoshimura (1927)

June 21, 1944

Depth (m)	Temp. (C)
0	14.67
2	12.20
4	10.59
6	9.51
8	8.92
10	8.27
12	7.03
14	6.43
16	6.25
18	6.11
20	6.03
22	5.42
25	5.01
30	4.85

August 11, 1944

Depth (m)	Temp. (C)
0	21.52
2	21.44
4	21.43
6	21.31
8	21.13
10	18.71
12	12.66
14	8.25
16	7.70
18	6.77
20	5.91
30	4.98
40	4.20
60	4.04
80	3.96
100	3.90
120	3.81

and Igarashi (1939). The lake is very famous for its beautiful landscape; it is situated at Chitose-mura, Chitose-gun in Hokkaido. Originating from the subsidence of earth's crust, the lake is a caldera lake. The elevation of the lake is 245 metres above sea level at the surface, covering the large area of 75.34 square kilometres, being about 15 kilometres in the largest diameter and about 3 kilometres in the least diameter. The maximum depth is 363 metres, being 265 metres in the mean, making it the second deepest lake in Japan, next to Lake Tazawa in Akita Prefecture. On account of the extraordinary poor productivity of phytoplankton, water is very clear, with blue colour, having 23.5 metres in the maximum transparency.

The temperature of the surface water is highest in August, rarely exceeding 22°C. Deep water below 100 metres measures slightly below 4°C even in summer. Previous investigations had all proved the existence of water of lower temperature than 4°C below 100 metres. This was also the case of the present investigation. The existence of cold water below 4°C, as discussed by Yoshimura (1930), is kept in stability in such a great depth where the pressure is very large. The temperatures recorded at the time of the present investigations are given in the tables in pages 7 and 8. In June the temperature decreases rather abruptly just below the surface, though there is no marked thermocline. However, the plankton is exposed to the change of temperature ranging about 9°C during migration up and down from the surface to 20 metre depth. In August a marked thermocline develops in 8-14 metre depth, so the plankton migrating through 0-20 metres is subjected to the change of temperature of more than 15°C. Thermocline sinks down to 15 or 20 metre depth in October in which the difference of the temperature between the surface and 20 metre depth becomes less, being only 1-2°C.

The water contains enough oxygen through the

October 20, 1944

Depth (m)	Temp. (C)
0	13.3
5	13.1
10	13.0
15	12.5
20	12.3
25	8.8
30	7.7

October 19, 1946

Depth (m)	Temp. (C)
0	13.74
5	13.75
10	13.70
15	13.56
20	13.53
25	10.43
30	6.22
50	4.06

depth down to the deep in any season, showing the maximum at 50 metre depth. The pH-value seldom becomes less than 7. Silicate content varies from 3.61 mg/l in winter to 13.5 mg/l in summer with very little difference according to the depth. Phosphate content fluctuates from about 6 mg/l to about 13 mg/l (Igarashi, 1939).

The quantity of plankton in this lake is very poor, but a copepod, *Acanthodiaptomus yamanacensis*, is usually frequent. Hayashi and Natori (1932) reported that this copepod (*Diaptomus denticornis yezoensis*=*Acanthodiaptomus yamanacensis*) displays a diurnal change of vertical distribution in this lake. Vertical distribution of plankton throughout the vertical range from the surface to 350 metre depth in Lake Shikotsu was observed by Tamura and Fuji (1949). They stated that *Daphnia longispina* is distributed above 50 metres, particularly shallower than 25 metres, and *Acanthodiaptomus yamanacensis* is distributed mainly around 25 metre depth, but it is found at such great depth as 250 metres. Ishida (1951), investigating on the exact quantities of plankton in this lake, found that the plankton is not always distributed uniformly even in such an oligotrophic clear lake as Lake Shikotsu.

Acanthodiaptomus yamanacensis is considered to be the main available food for a salmon named "Himemasu", which is the land-locked form of "Benimasu" or sockeye salmon, *Oncorhynchus nerka* (Walbaum), which has been one of the important sources of fishing production in the present lake since it was transplanted from Lake Akan in 1894. *Acanthodiaptomus* as well as other plankton seems to fluctuate in quantity from year to year owing to uncertain natural causes. Through the present investigation, occurrence of this species was very rich in summer of 1942, while it was poor in summer of 1943 but it recovered in the summer of 1944. The following table shows the number of *Acanthodiaptomus* caught in daytime of fine weather in three successive years. Numbers given are the total sum of the occurrences in a horizontal haul with five nets through the layers of 0, 5, 10, 15 and 20 metres (that is number of individuals in about 19 cubic metres). Again *Acanthodiaptomus* became rare in 1949, and remarkably decreased in 1950.

Date	Hour	Number of individuals
Aug. 20, 1942	9:40 a. m.	267340
〃	10:50 a. m.	238040
Aug. 15, 1943	9:00 a. m.	9830
〃	11:30 a. m.	17790
Aug. 10, 1944	9:00 a. m.	49730
〃	10:00 a. m.	57980
〃	12:00 m.	105480

Koikuchinoike of Tsugarujuni Lake Group

There is a group of small dammed lakes in Iwasaki-mura, Nishitsugaru-gun, Aomori Prefecture, in the area of four by four square kilometres, elevated 150-250 metres above sea level. The lakes are counted to the number of thirty three with four very small ponds; among them the lakes having an area exceeding 10000 square metres are twelve in number (Yoshimura and Koba, 1933; Yoshimura, 1934; Yoshimura, Koba and Osatu, 1934; Yoshimura, Koba, Obara and Osatu, 1934).

One of these twelve lakes, Koikuchinoike, on which the author has worked, is approximately round in shape, situated 202 metres above sea level, covering 47450 square metres. The largest diameter of the lake is 295 metres. Its depth is 14.2 metres in the mean and 23.3 metres in the maximum. Transparency of water is recorded as 1.3-2.0 metres in May, 3.3-3.6 metres in August and about 8.8 metres in December (Yoshimura, 1935b; Kokubo and Kawamura, 1941a; Kawamura and Kokubo, 1941b; Kawamura, 1947).

The surface temperature rises above 20°C in midsummer, but seldom attains 25°C (Yoshimura, 1935a; Kokubo and Kawamura, 1941a) and in early March it is recorded as 1.6°C under ice (Kokubo and Kawamura, 1941b). Thermocline is found in 10-15 metres in May after spring circulation period, but it comes up to 2-10 metres in July. This ascending of the thermocline is probably caused by a cold water spring which pours into the middle layer of the lake water from oneside of the basin. Water temperature at 10 metre layer is 10.5°C in the middle of May, while it declines to 5.9°C in the middle of July.

The pH value of water is usually in the maximum at the surface, sometimes at about 2 metre depth, declining gradually to acidic downwards. However, any sign of reversal of pH value in anaerobic hypolimnion has not been observed (Yoshimura, 1937a; Kokubo and Kawamura, 1941a, 1941b). According to the studies of Kokubo and Kawamura (1940a), buffer value of the water in the lake varies with depth, showing irregular distribution in the epilimnion (0-10 m), regularly decreasing in the hypolimnion (below 15 m). The value of cot α at the bottom layer becomes about four times as much as that at 2 metre layer.

The magnitude of buffer value seems due mainly to baron bicarbonate and carbonic acid of water. The value shows seasonal fluctuation, decreasing more in summer than in spring, especially being notable below 16 metres (Kokubo and Kawamura, 1940c).

Oxygen content decreases abruptly at metalimnion, and a remarkable anaerobic layer occurs in hypolimnion. Both the oxidation by bottom deposits and the putrefaction of bait thrown into the lake for rearing trout too excessively are responsible for the formation of this anaerobic condition (Kawamura and Kokubo, 1941a; Kokubo 1941c). There exists a little oxygen (0.9 % of saturation) in the bottom layer in May, but this is exhausted by June, the water below 20 metres becoming anaerobic. The thickest anaerobic layer develops in July, no oxygen being contained below 16 metres. The anaerobic layer is held below 16 metres during August, September and December. In March the water at 20 metres contains oxygen as 6.7 % of saturation, only the bottom water being anaerobic. Hydrogen sulphide is found at the bottom layer, the amount being recorded as 2.14 mg/l in June and 2.12 mg/l in July (Kokubo and Kawamura, 1941a). The declination of oxydation potential (rH) in the anaerobic layer which corresponds to the gradient of minimal oxygen quantity was studied by Kokubo (1941a, 1941c, 1942). According to him, rH value varies from 69 at 18.5 metre depth to 74 at the bottom.

Kokubo and kawamura (194 b) and Kokubo (1941b) reported thirty species of plankton from this lake. The quantities of plankton are very large; especially the occurrence of *Asterionella formosa* in May and June, *Melosira granulata* var. *angustissima* from September to December, and *Volvox aureus* in August is extraordinarily great.

As stated above, the present lake shows fair stratification in temperature and in other hydrographic conditions during the stagnation period, owing to its eutrophic character.

The temperature and pH value of the water observed in the afternoon on July 16, 1943, when the present observations on the diurnal movement of plankton through 0 12.5 metres were made, are given in the following table (The data are provided from practice observation by students). The difference of temperature between the surface and 12 metres is 19.3°C with a remarkable inclination in the 4-10 metre depth. So the plankton is exposed to the range of temperature above given during the migration from the surface to 12.5 metre depth.

Depth (m)	Temp. (C)	pH value
0	24.7	8.0
2	22.8	8.0
4	21.6	7.9
6	15.3	7.7
8	10.9	7.9
10	7.0	7.3
12	5.4	7.1
14	4.9	6.9
16	4.9	7.0
18	4.8	6.7
20	4.4	6.7
22	4.2	9.7

Of the oxygen content, according to Yoshimura (1937a) there was 0.11 cc/l at 20 metres on July 4, 1933, but it became anaerobic at this depth on July 27. Kokubo and Kawamura (1941a) found anaerobic layer below 16 metres on July 2, 1940, as given in the following table.

Depth (m)	Oxygen content (cc/l)	Saturation percentage of oxygen
0	5.94	92.7
2	6.80	104.8
5	6.72	96.1
8	8.40	100.4
10	4.19	47.8
12	2.52	28.3
14	1.54	17.1
16	0	0
18	0	0
20	0	0
22	0	0
22.5	0	0

(Kokubo and Kawamura, 1941 a)

The oxygen content at 12 metres was less than half of that at the surface. The plankton animals had to be subjected to this environmental change when descended to 12.5 metres in the present studies.

The transparency was recorded as 5.5 metres by the author on July 16. According to the study of Kikuchi (1935), at the depth at which the Secchi's disc gets out of sight the illumination diminishes to 14.5 % of that just under the surface. Therefore, in the present case, the underwater illumination at 5.5 metre depth should be roughly 14.5 % of that of the surface.

IV. Materials Dealt with in the Field Observations and in the Laboratory Experiments

The following one copepod and three cladocerans were observed on their diurnal migration at Lake Shikotsu, and they were also used in the laboratory experiments on their tropism.

Acanthodiaptomus yamanacensis (Brehm)
Syn. *Diaptomus denticornis* var. *yezoensis*, Kokubo
Diaptomus pacificus, Kokubo
Acanthodiaptomus pacificus, var. *yamanacensis*, Kikuchi
Daphnia longispina O. F. Müller subsp. *hyalina* (Leydig)
Scapholeberis mucronata (O. F. Müller)
Bosmina coregoni Baird

According to Kokubo (Tanakadate, 1925), nauplii of *Diaptomus denticornis* var. *yezoensis* appear from May and increase to the maximum occurrence in late June at Lake Shikotsu. Metanauplii are found from June, becoming most numerous in July. Copepodids are also found abundantly in July. Most of them develop to adult in August, and in September they all grow to adults. Adult animals breed in October, and almost disappear by the middle of November.

In the present field observation *Acanthodiaptomus* collected in late June, 1944, were all

copepodids of 0.48–0.69 mm, averaging 0.59 mm, in total length, and with only three pairs of swimming feet. They developed in the middle of August to copepodids of 0.83–1.03 mm, averaging 0.92 mm, in total length with four pairs of three-segmented swimming feet and a rudimental fifth foot. In August adult forms composed of about 11 % females and 29 % males for total were collected together with the copepodids to the amount of 60 %. Body length of the females was 1.36–1.19 mm, 1.27 mm in average and that of the males was 1.09 1.00 mm, 1.04 mm in average. The collection of late October in that year and in 1946 included adult forms only, of which the females were 19 % in number in 1944 and 23 % in 1946 respectively.

The adult females of this species are easily distinguished from the males, as the former are provided with a lateral prominence on the last thoracic segment, while the latter have right geniculated antenna. In the present investigation, the number of adult females, adult males and copepodids was calculated separately in all observations excepting the first preliminary one. The number of all other species was counted without separating by sex owing to the difficulty of rapid distinguishing. In *Daphnia longispina* subsp. *hyalina* and *Scapholeberis mucronata* scarecely any male individuals were found throughout the observations. *Bosmina coregoni* was collected in a large number only in one observation in October, 1946. The sex ratio of this species at that time was about 60 % for the females and 40 % for the males.

In the summer collection (1943) at Koikuchinoike of the Tsugarujuni Lake Group, the following five species were observed.

Acanthodiaptomus yamanacensis (Brehm)
Cyclops strenuus Fischer
Eucyclops prasinus (Fischer)
Daphnia longispina O. F. Müller subsp. *longispina* s. str.
Bosmina longirostris (O. F. Müller)

The ratio of the number of adult females, adult males and copepodids of *Acanthodiaptomus yamanacensis* was 13 : 7 : 80. The adult females, males and copepodids of *Acanthodiaptomus* were counted separately, but in the other four species counting of number of individuals was done without distinguishing the sex and developmental stages. *Daphnia longispina* subsp. *longispina* was extraordinarily abundant in this season as reported by Kokubo (1941b), and it was noticed that they were all females. The number of *Cyclops strenuus* was not very large, and the males occupied 7 % in number for 93 % of both females and young. *Eucyclops prasinus* was very rare, and probably the females only, some carrying eggs. The ratio of number of the females and the males in *Bosmina longirostris* was about 74 : 26.

V. Method of Field Observations

In order to get plankton animals simultaneously from various layers of water, samplings were made by the aid of parallel hauling of a series of plankton nets. Six or five ordinary plankton nets (23 cm in diameter of mouth ring; made of bolting cloth having 56.5 meshes to an inch) were attached to a cotton rope at various intervals. The weight at the end of rope was to be heavy enough to keep it vertical during towing. Thus the different nets were towed simultaneously through the different layers of water. Although, the nets were not equipped with closing apparatus, each net was attached to the rope in such a manner as both upper and lower parts of the mouth ring come in direct contact with the rope, so as to prevent contamination of samples from other layers. The distance of towing covered 100 metres at Lake Shikotsu, but at Koikuchinoike the towing of nets was made for only 10 metres, by which sufficient samples could be obtained.

VI. Results of Field Observations

(1) Vertical Distribution in Deep Water of Lake Shikotsu

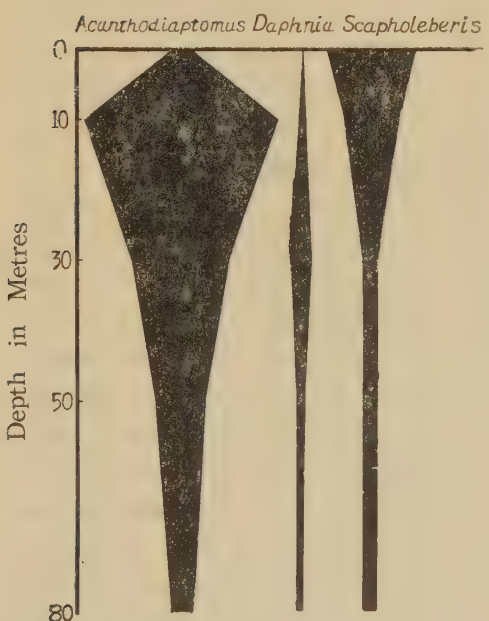


Fig. 1. Vertical distribution of plankton crustaceans at 10:30 a. m. on August 20th, 1942, under bright sun in the deep water of Lake Shikotsu (Observation 1)

Observation 1 (Table 1, Fig. 1)

A simultaneous towing with five nets through 0, 10, 30, 50 and 80 metre depths was made in the deep water region of Lake Shikotsu at 10:40 a. m. on October 20, 1942 under a bright clear sky. The results show that *Acanthodiaptomus* was distributed very rarely at the surface, becoming largest in number at 10 metre depth. The number was diminishing at depths below 30 metres. Of *Daphnia* no individual was found from the surface layer while it occurred in the maximum at 30 metre depth. *Scapholeberis*, in contrast with the adove forms, was found in the greatest number from the surface, having considerably decreased at 10 metres, and it became very rare in the water deeper than 30 metres.

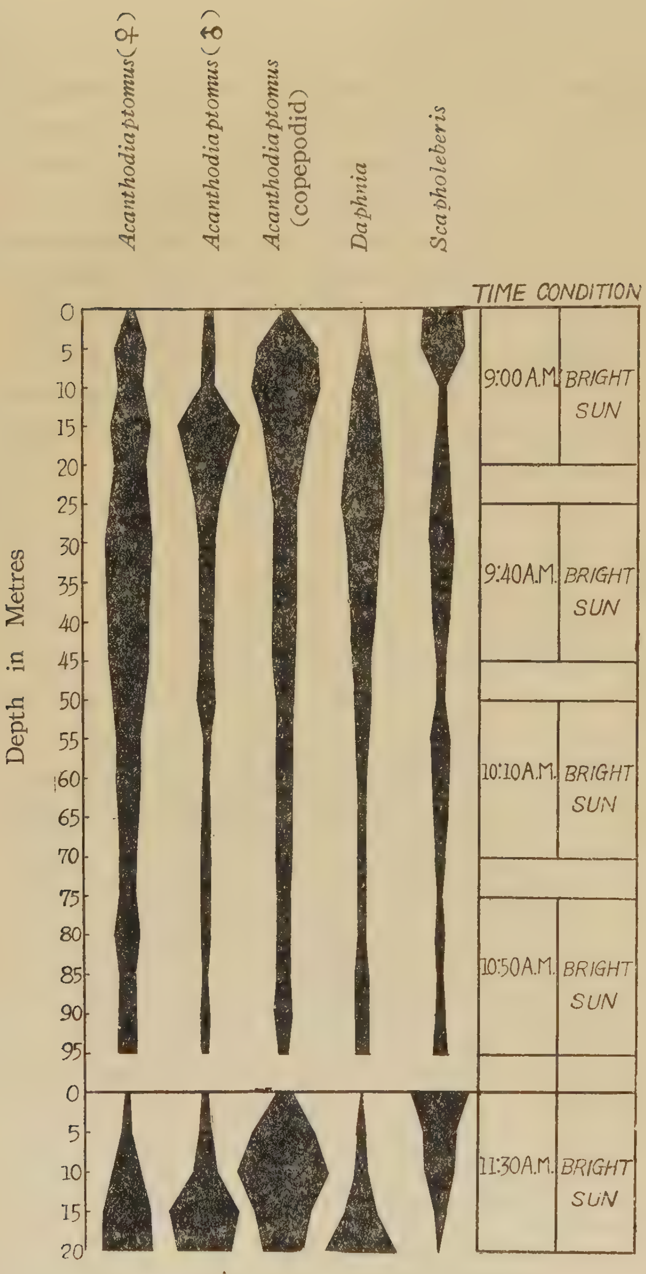


Fig. 2. Vertical distribution of plankton crustaceans in daytime under bright sun on August 15th, 1943, in the deep water of Lake Shikotsu (Observation 2)

Observation 2 (Table 2, Fig. 2)

The second observation at deep water region was carried out at 9 : 00-11 : 40 a. m. on August 15, 1943, under bright sun. The collections were performed at every five metre depth covering 0 95 metres. As the simultaneous towing with five nets can collect the plankton from five layers at the same time, the towing had to be repeated four times for collecting from 0-20 m, 25-45m, 50-70m and 75-95m. It was necessary to spend about two hours from 9 : 00 a. m. to 10:50 a. m., which was rather too long and the animals would possibly change the distribution during this time, and so an additional towing at 0-20 metres was again made after the primary four series of collections were accomplished.

The distribution of the female *Acanthodiaptomus* was comparatively uniform from the surface to the deep, especially keeping approximately constant number from 5 metres to 50 metres. Comparing the distribution in 0-20 metres at 9:00 a. m. with that at 11:30 a. m., it was indicated that the number at 5 metres became very small after two hours. The males showed a conspicuous stratification as compared with the females. They were very rare in the water above 10 metres and increased in number abruptly at 15 metres and a remarkable decreasing was seen below 25 metres. The number of animals distributed below 55 metres was very small, and only two individuals were found from 95 metre depth. The maximum

distribution was seen at 15 metre depth both at 9:00 a. m. and 11:30 a. m. The copepodids occurred at 5 10 metres in great number, though they were not abundant at the surface. The number decreased below about 15 metres. Thus, it was indicated that the copepodids were abundant in shallow water, while the adult females were distributed in all depths and males occurred in rather restricted zone, i. e. about 15 metre depth.

No individuals of *Daphnia* were found at the surface. Gradual increasing was seen from 5 metres to 15 metres, with the maximum at the latter depth. Below this level they again commenced to decrease. At 11:30 a. m. ratio of the number in 0 10 metres to that in 15 20 metres became greater than at 9:00 a. m., showing the downward migration of the animals during the course of two hours.

Scapholeberis was found abundantly in 0 5 metres and rapidly decreased below 10 metres at 9:00-10:50 a. m. At 11:30 a. m., the number at the surface layer was greater than at 9:00 a. m. and reached the maximum, though some remained even in deeper layers.

Observation 3 (Table 3, Fig. 3)

The third observation in the deep water region was carried out at 12:20 12:50 p. m. on October 18, 1946, under heavy clouds and then at 11:20 a. m. - 12:00 m. on October 19 under the bright sun. The collections in both cases were composed of two series of 10 minute haul. The first haul was done for the layers of 0, 5, 10, 15, 20 and 25 metres and the second one for 25, 30, 35, 40, 45 and 50 metres respectively. In expressing the results by diagram of figure 3, the number of individuals at various depths obtained in the second series of haul was corrected by comparing the value obtained at 25 metre depth in the first haul with the value in the second haul.

The female *Acanthodiaptomus* had approximately uniform distribution through 0-50 metres under heavy clouds, although the number became large with the depth down to 40 metres, in which the maximum was found (the collections at 30 metres and 35 metres were unsuccessful), but it decreased again gradually below 45 metres. On the contrary, in fine weather it was very rare in 0-10 metres, increasing from 15 metre layer until it got the maximum at 20 metres. Below 25 metres the number again decreased with the depth. The number of animals became less below 40 metres in fine weather than in cloudy. The type of distribution of the male *Acanthodiaptomus* under heavy clouds, differing from that of the females, was expressed in the diagram as a pillar with swelling in the middle portion. The maximnm number was found at 15 metres. In the fine weather a remarkable stratification was seen, the animals having decreased in 0 5 metres, slightly increased at 10 metres, and abundantly in 15 20 metres. Down to 25 metres the number decreased again and became very small below 30 metres. The number of the animals hardly varied below 40 metres in the fine weather as compared with that in the cloudy. It was perceived that the males were easily affected by light than the females, the vertical distribution of the males having changed conspicuously with change of weather. The vertical distribution of adult *Acanthodiaptomus* in both sexes in the fine weather in autumn did not greatly differ from the

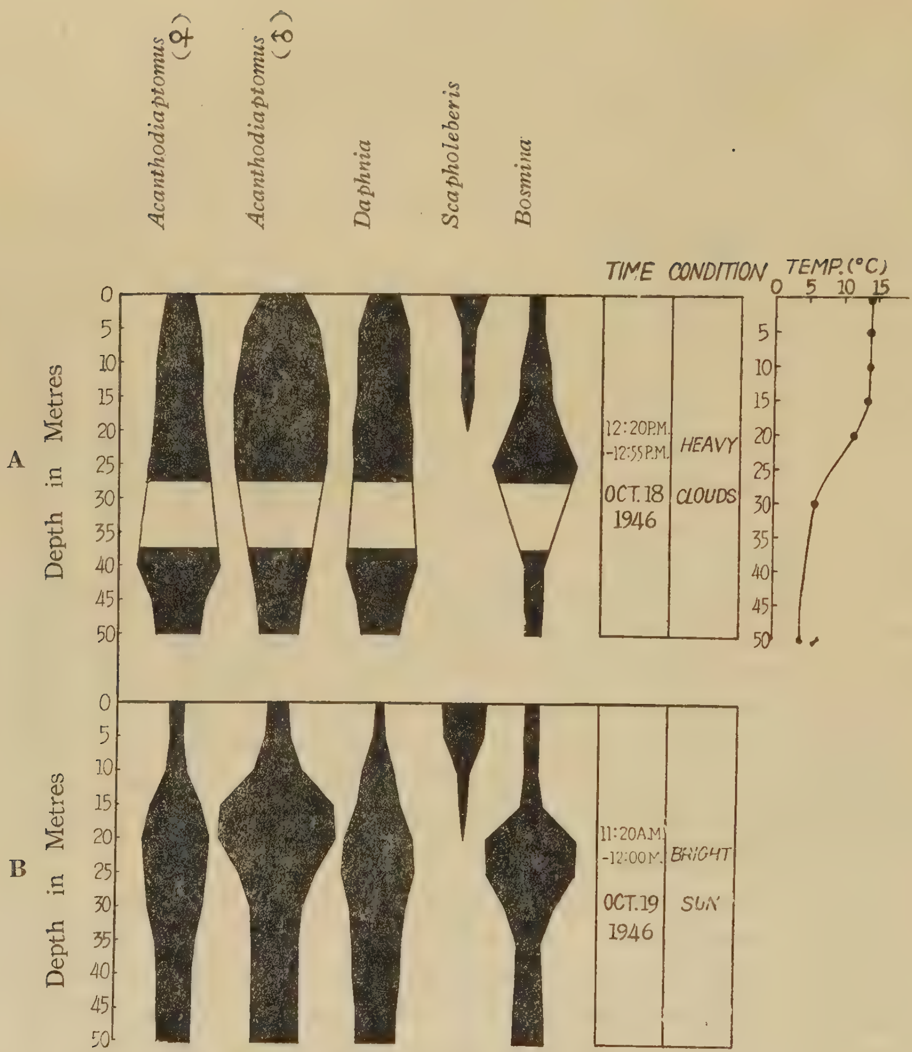


Fig. 3. Vertical distribution of plankton crustaceans in daytime in October, 1946, in the deep water of Lake Shikotsu (Observation 3)
(A) Under heavy clouds on Oct. 18th
(B) Under bright sun on Oct. 19th

distribution in summer (Obs. 2), despite the fact that the surface temperature fell from 21.5°C in summer to 13.7°C in autumn, and the thermocline was found in 8-14 metres in summer, while it descended below 20 metres in autumn.

Daphnia showed a nearly uniform distribution under heavy clouds, though the number at the surface was about one-sixth of that at 5 metres. The distribution in the fine weather was nearly the same as that of the femals *Acanthodiaptomus*, but the maximum layer was at 25 metres.

Scapholeberis was not collected from the layers below 20 metres. It always crowded in the surface water.

Bosmina had the maximum distribution in 20-25 metres in both fine and cloudy weather. However, the stratification of the distribution became very distinct in the fine weather.

(2) Diurnal Migration in Lake Shikotsu

From the above observation (Obs. 3) it became clear that plankton crustaceans in Lake Shikotsu, except *Scapholeberis*, manifest vertical movement at least down to 50 metres, particularly remarkable above 20 or 25 metres, according to the light condition, e. g. cloudy or fine weather. To ascertain the diurnal migratory habit the repetition of collections by parallel haul with a series of nets through the layers of 0-20 or 0-25 metres were attempted at hour intervals. Unfortunately, the collections had often to be given up on account of the strong wind and high waves.

Observation 4 (Table 4, Fig. 4)

The observation was made on the 20th and 21st, August, 1942. The weather was quite bright from the morning of the 20th, but it became rather cloudy after about 5:00 p. m. It was still twilight at 6:00 p. m. after the sun had set. In the first day the collections were performed nine times between 8:40 a. m. and 6:00 p. m. The work on the boat was hardly carried out without lantern at 6:50 p. m. in the dusk. The wind blew from 7:00 p. m. and the collection had to be given up. As the lake became calm again before dawn of the next morning, collections were begun at. 3:00 a. m., and performed seven times until 8:50 a. m. in quite calm. The day dawned about 4:00 a. m. and the sun rose on the mountain at 4:40 a. m. Soon heavy clouds appeared, which did not lift until the work was finished.

As given in figure 4, *Acanthodiaptomus* was very rare above 5 metres, showing the maximum at 15 metres, before noon on the 20th in bright weather. At 2:30 p. m. the animals migrated up in a large number to 10 metres and increased more above 5 metres than before. At 4:00 p. m. a considerable number of the animals appeared both at the surface and 2 metres, but abundant animals were still distributed nearly uniformly below 5 metres down to 20 metres. After 5:00 p. m. the maximum number was almost always seen at the surface, and at 4:40 a. m. on the 21st the number at the surface was more increased although the sky was light. Under heavy clouds about 6:00 a. m. the animals were distributed uniformly through all layers, but after 7:30 a. m. they made some descent even under heavy clouds.

Daphnia was distributed mostly below the thermocline at 10 metres during daytime on the 20th. In darkness before dawn on the 21st some of the animals appeared also at the surface, and in the morning of heavy overcast some of them appeared at 2 metres, though their maximum occurrence was found at 15 metres.

Scapholeberis, contrary to *Acanthodiaptomus*, was found abundantly at the surface in daytime. It also occurred in considerable number in the surface at night too.

Besides the above species, 58 individuals of *Bosmina coregoni* were collected from 20 metre layer at 6:00 p. m. on the 20th, though none was found in other collections.

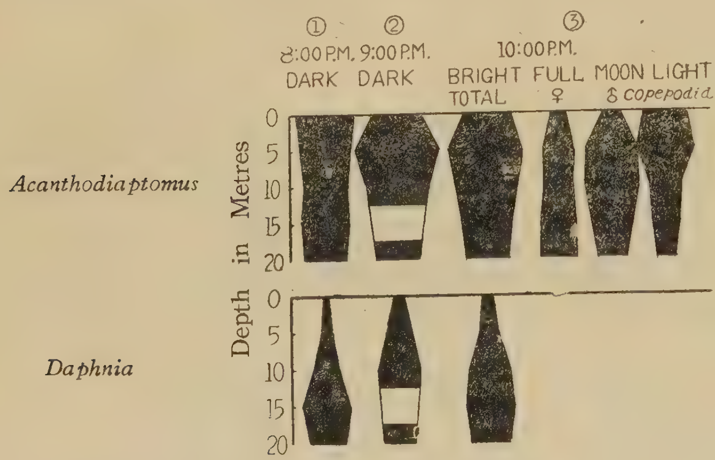


Fig. 5. Vertical distribution of plankton crustaceans at night on August 14th, 1943, in Lake Shikotsu (Observation 5)

Observation 5 (Table 5, Fig. 5)

Three collections at night and one in daytime were carried out on August 14 and 15, 1943. The result of daytime collection through the surface down to 95 metres has already described on p. 14 (Obs. 2). It was quite dark at 8:00 p. m. and 9:00 p. m. when the first and the second collections were made. But when the third collection was done at 10:00 p. m., bright full moon shone in the clear sky.

The adult females of *Acanthodiaptomus* were distributed nearly uniformly at 10:00 p. m., though they increased in number with the depth. However, the males occurred in a large number in 5 10 metres, decreasing above and below that level. The copepodids occurred abundantly in 0-5 metres, decreasing in lower layers. Comparing the above results with that of the distribution in daytime (Obs. 2), it is clear that *Acanthodiaptomus* swarm up at night; especially upward migration of the males was remarkable.

Daphnia also ascended to the surface at night, though a large number were still found below 10 metres. It happened that there was some ascending at 9:00 p. m. as compared with the state at 8:00 p. m. However the animals again descended at 10:00 p. m., probably being affected by the moon light.

Scapholeberis was found in very small number in this collection.

Observation 6 (Table 6, Fig. 6)

The observation was carried out on the 20th-22nd in June, 1944, when we have the longest daytime of the year. The collections both 2:00 p. m. on the 21st and 12:00 m. on the 22nd were made near the coast at depths shallower than 25 metres due to the atrundum gale, while others were carried out in the deeper water. The surface temperature was 14.67°C and it decreased gradually to the deep (p. 7). The thermocline was not

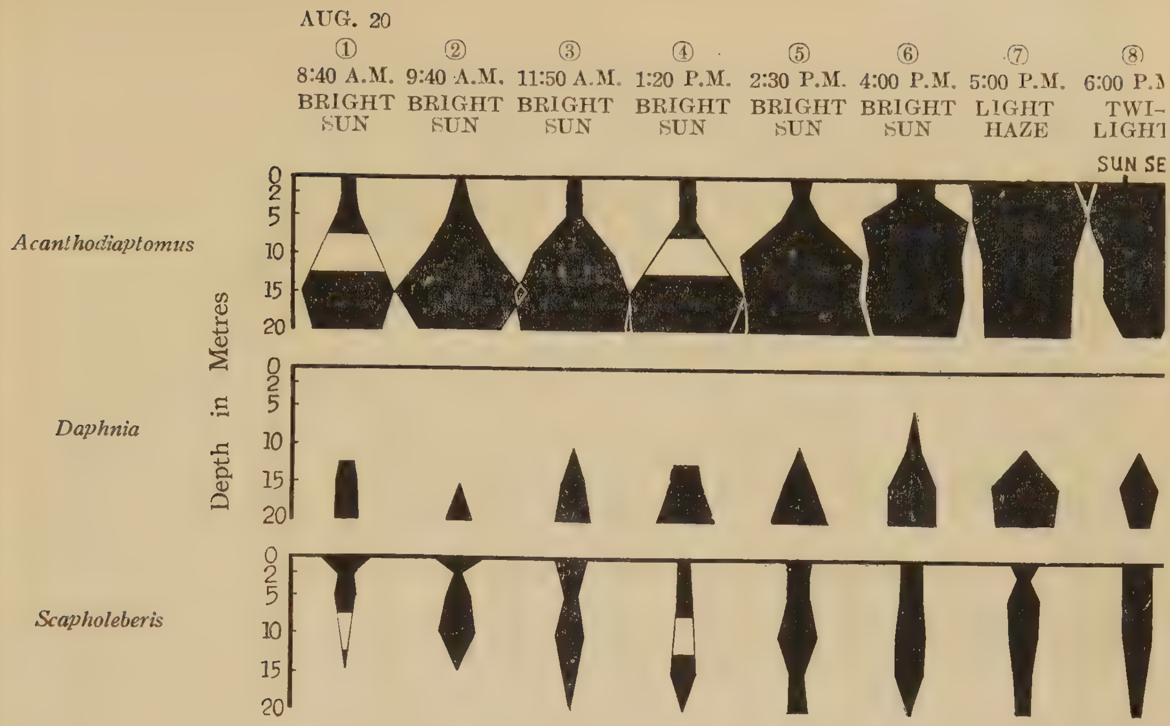
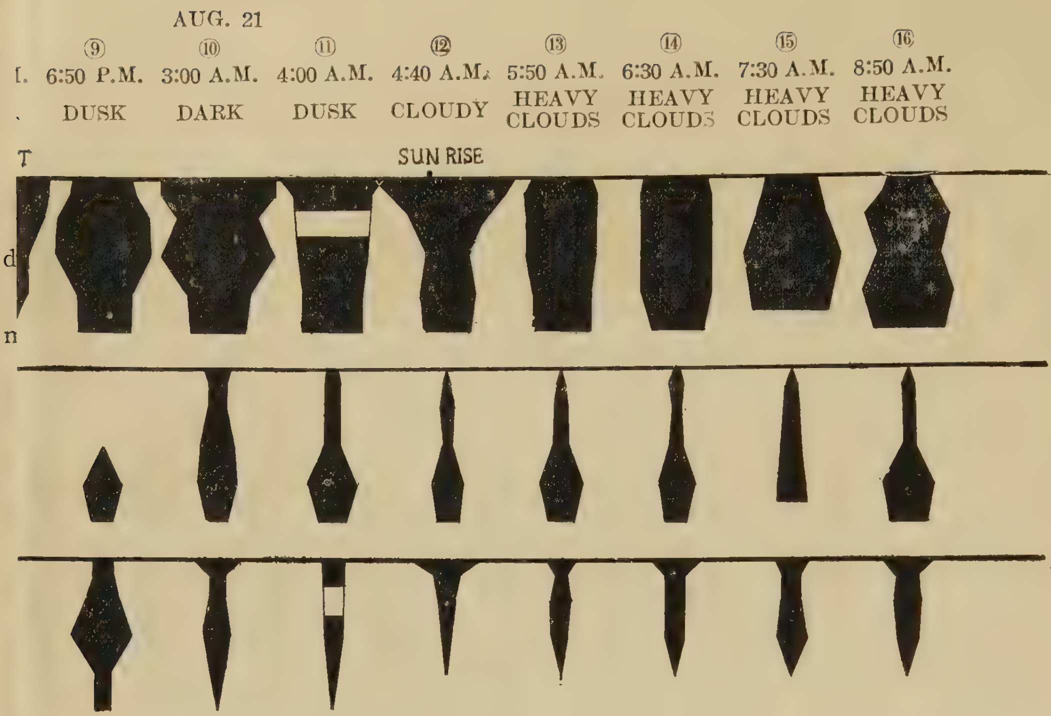


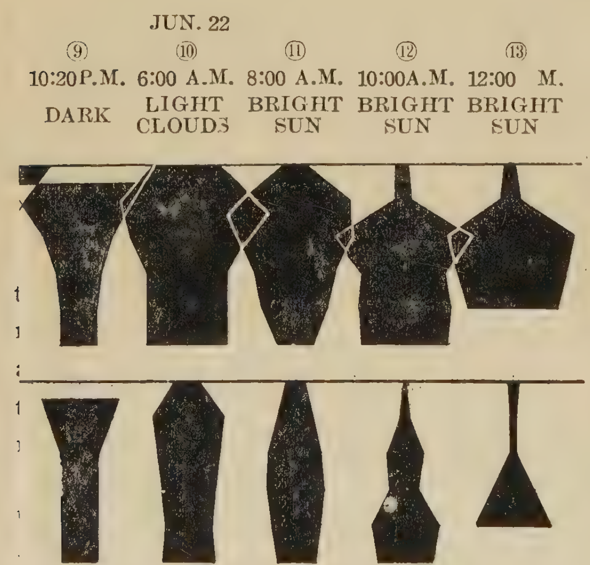
Fig. 4. Diurnal migration of plankton crustaceans in August 20th—2

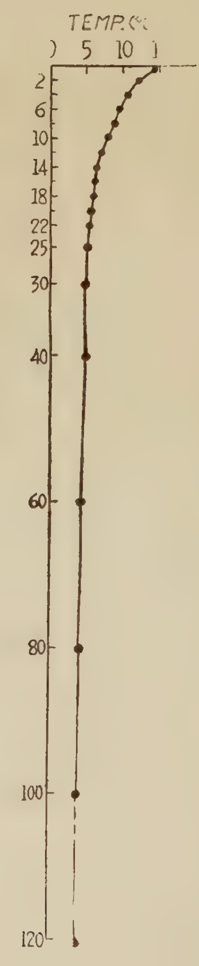


Fig. 6. Diurnal migration of plankton crustaceans in June 20th—22nd



1st, 1942, in Lake Shikotsu (Observation 4)





, 1944, in Lake Shikotus (Observation 6)

conspicuous at this time. The sun was already high at 6:00 a. m. and shone on the lake. The sun set behind the mountain at about 6:50 p. m., but it was not dark until 8:30 p. m.

Acanthodiaptomus was still all in copepodid stage at this time. The animals abundantly occurred in 0–5 metres both at 6:00 a. m. and 6:00 p. m., although the sky was bright. Comparing the distribution in the bright afternoon on the 20th with that on the 21st in heavy clouds, the latter showed a remarkable crowding at shallow layers. It was very bright at 10:00 a. m. on the 21st and animals crowded abundantly at 10 metres, escaping from the surface, differing from the distribution at the same hour of the 20th under light clouds. At night (10:20 p. m. on the 21st) the number at 5 metres was a little larger than below 10 metres.

Daphnia was abundantly distributed below 10 metres in daytime. At 4:00 p. m. there was no individual at the surface, while the maximum number was present at 15 metres both on the 20th and the 21st. The population of *Daphnia* collected on these days was composed of a small number (10 %) of larger individuals (1.96-1.36 mm, averaging 1.59 mm in length of carapace) and an abundant number (90 %) of small ones (0.92 0.50 mm, averaging 0.65 mm). Under any condition larger specimens seem to prefer comparatively deep water, not being found at the surface.

Scapholeberis and *Cyclops strenuus* were also collected at times though in a small number.

Observation 7 (Table 7, Fig. 7)

The seventh observation was the most laborious task to get the entire features of migration throughout day and night. Every-hour collections were begun at 7:00 p. m. on August 9th, 1944, but the work had to be stopped due to the wind which broke about 2:00 a. m. followed by rain. The lake became calm by the next morning, and the collections were again continued from 9:00 a. m. to 3:00 p. m. on the 10th. On the 11th the collections were carried out from 4:00 a. m. to 8:00 a. m. and from 3:00 p. m. to 5:00 p. m. The last series of collections was made from 6:00 a. m. to 8:00 a. m. and at 10:00 a. m. on the 12th. It was quite fair in the daytime on the 9th and the sunset was at 6:18 p. m. It became dusk at about 7:00 p. m. and the naked eye could not read the watch at 7:35 p. m. The sky became completely dark at about 8:00 p. m., then it again became light at 10:55 p. m. as the twenty-day moon rose to be covered with clouds after about 1:00 a. m. It was fair from the morning on the 10th, except slight clouds at about 1:00 p. m. It was still dusk at 4:00 a. m. on the 11th, when one could not read his watch. The sky became light at 5:00 a. m. and the sun rose at 5:52 a. m., shining upon the lake. In the seventh observation the position of collections was settled nearer to the coast than in the observation in August 1942 (Obs. 4), and so the sun's illumination of the surface of the lake was delayed a little. The sky was almost cloudless in the morning of the 11th, but covered with heavy clouds in the morning on the 12th and rain began to fall at 10:00 a. m. The surface temperature was 21.52 °C and the thermocline existed in 8 14 metres (p. 7, Fig. 7).

The female *Acanthodiaptomus* became rare at the surface late at night and almost disappeared from there after dawn (but some of them remained at the surface at 6:00 a.m.), while it showed nearly uniform distribution in midnight. The number in lower layers increased with the lapse of time in the morning and the animals almost disappeared even at 5 metres at 10:00 a. m. No animal was found in 0 10 metres at noon, the majority having crowded below 15 metres. Upward migration seemed to begin at about 1:00 p. m., and when it became dusk the maximum number occurred at 5 metres. A similar distribution was continued at 8:00 p. m. in darkness. The distribution became more or less uniform through vertical range at 9:00 p. m. The distribution under heavy clouds at 8:00 a. m., 10:00 a. m. and 3:00 p. m. showed that the animals remained in upper layers more than in the fine weather.

The distribution of the males was restricted to some definite layers as compared with the females. Most of the males were distributed in 0-10 metres from midnight to dawn, showing a large difference of number between the upper and lower layers contrary to the females. The maximum layer descended to 10 metres at 7:00 a. m. and to 15 metres at 9:00 a. m. At noon a large number was seen in 15-20 metres, almost disappearing in 0 10 metres. Most of the animals still remained at 15 metres at 1:00 p. m., differing from the distribution of the females. However, the beginning of upward movement had already taken place at this time. A large number of the animals ascended to 10 metres at 2:00 p. m., reaching to the maximum at 3 : 00 p. m. The maximum layer was found at 5 metres from 7:00 p. m. to midnight, though there was a great difference in number between 5 metres and other depths at 7:00-8:00 p. m. as compared with that of the females.

In the copepodids there was no marked difference of distribution in any layers at midnight, though the maximum number was found at 5 metres. Then the maximum depth moved downward as time passed. After the sun shone upon the lake, the number at the surface decreased, the maximum layer being at 10 metres at 7:00 a. m. As the sun rose higher, the animals migrated into deeper water. They became very rare in number at 0-5 metres. At about noon the maximum occurrence was at 15 metres. Ascending movement in the afternoon had already begun at 2:00 p. m. and a large number occurred at 5 metres at 3:00 p. m. At about one hour before sunset the maximum distribution was found at the surface and it descended again to 5 metres in darkness.

Daphnia collected in this time comprised individuals of which the length of carapace was 1.63 0.68 mm, being 1.15 mm in average. The diurnal migration of *Daphnia* was very regular. There were about the same number at each layer from 15 to 20 metres, but rarer above 10 metres, a few appearing at the surface at 7:00 p. m. on the 9th. The maximum depth rose to 15 metres at midnight. During the dark night, however, there was also a large number at 10 metres and still a considerable number in 0 5 metres. The animals appeared abundantly also at the surface at 1:00 a. m., showing nearly uniform vertical distribution. A slight downward movement was noticed at 2:00 a. m. The animals became very rare in 0 5 metres at 9:00 a. m. with the maximum layer below 20 metres.

This distribution was maintained throughout the daytime. A similar distribution was observed at 4:00 a. m. on the 11th and 3:00 a. m. the day before. At 5:00 a. m. the animals descended slightly, and all of them disappeared from the surface at 8:00 a. m., the maximum layer going down below 20 metres. Even under heavy clouds in the afternoon (3:00 p. m. and 4:00 p. m. on the 11th) no animal was found at the surface until some of them appeared at 5:00 p. m. However, in the morning (6:00 a. m. to 10:00 a. m.) on the 12th under heavy clouds the animals were found in comparatively larger number than under the bright sun in the morning of the preceding day below 15 metres. The maximum layer was found at 10 metres at 6:00 a. m., while this moved down to 20 metres at 8:00 a. m. In the summer of 1948 (Obs. 4) *Daphnia* almost disappeared above 10 metres in daytime, while they were found there in considerable number in the present observation. Some of the animals were found even at less than 5 metres in the present case.

Scapholeberis appeared always abundantly at the surface, though the collections at night often times did not include specimens from any layer.

In addition, *Bosmina coregoni* was found abundantly from 20 metres at 7:00 a. m. on the 9th.

Observation 8 (Table 8, Fig. 8)

The eighth observation was performed two times in the evening on the 20th and four times in the morning on the 21st October, 1944. The daytime was very short at this season. It was dusk at 5:00 p. m. on the 20th, the sun having set at about 4:30 p. m. The hands of a watch could scarcely be seen at 5:00 p. m. and to read the time was impossible at 5:25 p. m. In the morning on the 21st the light was suffecient to allow the reading of the watch at 5:20 a. m., and the sun rose at about 6:10 a. m. The sun was covered by clouds until about 6:30 a. m., but it shone after that time. The altitude of the sun at this season was about 19°at 8:00 a. m. and about 32°at 10:00 a. m., while it was about 35°at 8:00 a. m. and about 55°at 10:00 a. m. in summer (Aug. 10). The temperature of the surface wtaer was 13.3°C and the thermocline was present below 20 metres (p. 8, Fig. 8).

Acanthodiaptomus had all grown to the adult stage at this season. The vertical distribution both of the females and males showed that the largest number occurred at the surface at 5:00 p. m. on the 20th. They were more concentrated at the surface in darkness at 6:00 p. m. There was shown still a uniform distribution in twilight at 6:00 a. m. on the 21st, and then the animals slightly decreased at the surface at 7:00 a. m. under the bright sun. At 8:00 a. m. the number at the surface still continued to decrease, though the distribution below 5 metres hardly varied. The maximum layer went down to 15 metres at 10:00 a. m., but a considerable number of the animals still remained at the surface. Comparing the migration of the females with that of the males, it was found that the number of males in shallow layers in dawn or darkness was greater than that of the females, while that of the males in the deeper layers (below 5 or 10 metres) in

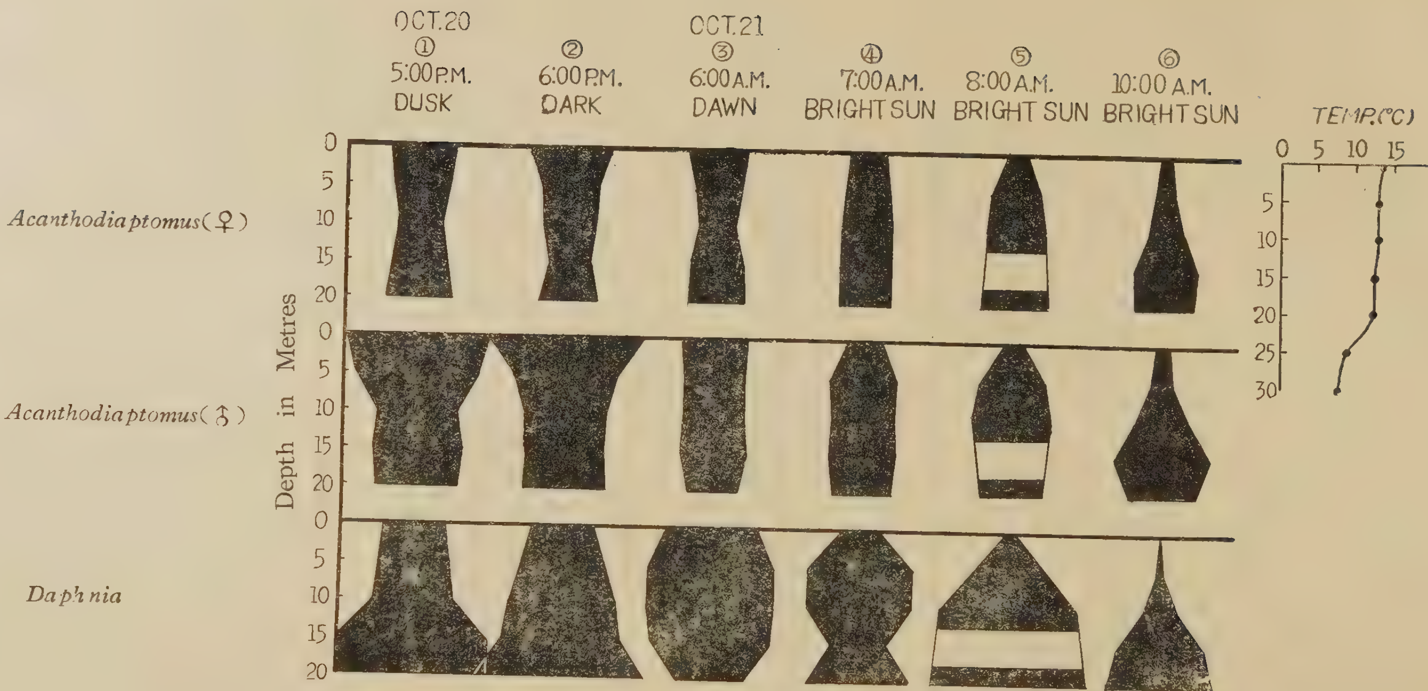


Fig. 8. Diurnal migration of plankton crustaceans in October, 1944, in Lake Shikotsu (Observation 8)

daylight was greater than that of the females.

Daphnia occurred at the surface in some number in dawn and darkness, though the largest number was still found in the deepest layer. *Daphnia* became very rare in the shallow layers at 8:00 a. m. under the bright sun. The animals were absent at the surface but a few were found at 5 metres at 10:00 a. m. They were more frequent in shallow layers than in summer. (Compare the distribution at 6:00 a. m., 7:00 a. m. and 8:00 a. m. on the 21st October with that observed at the corresponding hours in summer, Obs. 7)

(3) Diurnal Migration in Lake Tsugarujuni

Observation 9 (Table 9, Fig. 9)

The observation now described was made at Koikuchinoike in the Tsugarujuni Lake Group in July, 1943. The collections were carried out fourteen times usually at intervals of four hours from the evening of July 18th to the evening of the 20th. The nets were hauled through six layers every 2.5 metres from the surface down to 12.5 metres. Materials observed in the present collection included five species, of which *Daphnia longispina* subsp. *longispina* was most abundant.

It was quite clear during the daytime on the 18th, but became cloudy at 4:00 p. m. At 8:00 p. m. the sky became dark and the moon was not clear with thick cloud. At midnight the cloud was cleared and the full moon (16 days in age) was shedding her rays on the lake. At dawn (4:00 a. m.) on the 19th there was enough light to allow work. At 8:00 a. m. the sun hung high and it was bright the whole day. The sun was still bright in the sky at 4:00 p. m. Twilight faded away before 8:00 p. m. The moon had not yet risen at this time and so the sky was too dark to allow the reading of a watch. At midnight the moon was faint due to cloudy weather, but the clouds became thin at 3:00 a. m. on the 20th to permit the reading of the watch by the moon light. The sky was clear and there was enough light at 4:00 a. m. The day was quite fine both at 8:00 a. m. and 4:00 p. m., while the sun was covered with light clouds at noon. The intensity of light at nightfall at 8:00 p. m. seemed to be nearly similar to that at daybreak at 3:30 a. m.

The adult females of *Acanthodiaptomus* always remained in a considerable number at 2.5 metre depth even when most of them left the surface layer (excluding the distribution at 0:00 a. m. on the 19th), and the maximum layer existed at 5 metres through all day and night. They descended during the time from 4:00 p. m. to 8:00 p. m. on the 18th, but ascended during this time on the 19th. The distribution at 0:00 a. m. on the 19th as comapred with that at 8:00 p. m. on the 18th showed clearly that they descended on account of the light of the moon. The ratio of the number at 5 metres to that at the surface was greater at midnight of the 19th under the dim light of the moon than at 8:00 p. m. The animals rather ascended from 0:00 a. m. to 4:00 a. m. on both the 19th and the 20th, although the light of dawn at 4:00 a. m. was more intense than the moon light at midnight. Moreover, the animals were distributed in shallower layers at 4:00 a. m.

than at 3:00 a. m. on the 20th. They migrated downward from 4:00 a. m. to 8:00 a. m. on both the 19th and the 20th, especially intensively in the latter case. At noon on the 19th they disappeared from the surface and on the 20th they had already left the surface at 8:00 a. m., having nearly a similar distribution at noon. The animals showed an upward migration, until 4:00 p. m. on both the 19th and the 20th. Through all hours the shallowest distribution was seen at 4:00 a. m. and 8:00 p. m.

The maximum number of the adult males was always found at 5 metres as in the females. They ascended remarkably from 4:00 p. m. to 8:00 p. m. on both the 18th and the 19th. The descending migration was clearly shown at midnight (0:00 a. m. on the 19th) due to the light of the full moon. However, this was not the case at 0:00 a. m. on the 20th under the dim moon light. The distribution at 0:00 a. m. and 4:00 a. m. on the 19th was nearly the same, though the animals occurred only at 5 metres at 4:00 a. m. on the 18th. While the distribution at noon and 4:00 p. m. was nearly the same on the 19th, the animals showed an ascending migration at 4:00 p. m. on the 20th even under the bright sun as compared with at noon when the sun was covered with light clouds. The descending movement due to the moonlight was more remarkable in the males than in the females. Namely the males were more sensitive to the slight change of luminosity than the females as shown in the observations at Lake Shikotsu.

The copepodids were hardly found at the surface, only a very few individuals being collected there in a few cases. They occurred in some number at 2.5 metres, but in large number below 5 metres during daytime. They did not make notable vertical migration.

The vertical distribution of *Cyclops strenuus* varied remarkably with hours. The animals occurred in a larger number in shallow layers than in deeper at 4:00 p. m. on each day. The number of individuals at the surface at 4:00 p. m. on the 18th under cloudy sky was larger than that at the same hour on both the 19th and the 20th under the bright sun. The number at the surface slightly increased from 4:00 p. m. to 8:00 p. m. on the 18th and the 19th, though the distribution was rather uniform throughout vertical range. At midnight the animals showed generally a uniform distribution. However, the maximum layer existed at 7.5 metres at 0:00 a. m. on the 19th under the bright moon light. The animals were also abundantly found at the surface at 3:00 a. m. and 4:00 a. m., though some of them migrated downward. They clearly descended at 8:00 a. m. on both the 19th and 20th to cause the maximum population in the deepest layer observed (12.5 m). A similar distribution was shown at noon. Thus the present species apparently increased in number in the lower layers from 8:00 a. m. to 4:00 p. m., but was distributed nearly uniformly throughout the vertical range from the evening dusk until dawn.

Eucyclops prasinus appeared only in a small number. The animals apparently descended below 2.5 metres in daytime and appeared at the surface at night.

Daphnia longispina subsp. *longispina* was very abundant, bulking large in the samples. The animals were distributed in the maximum number at 5 metres and comparatively less

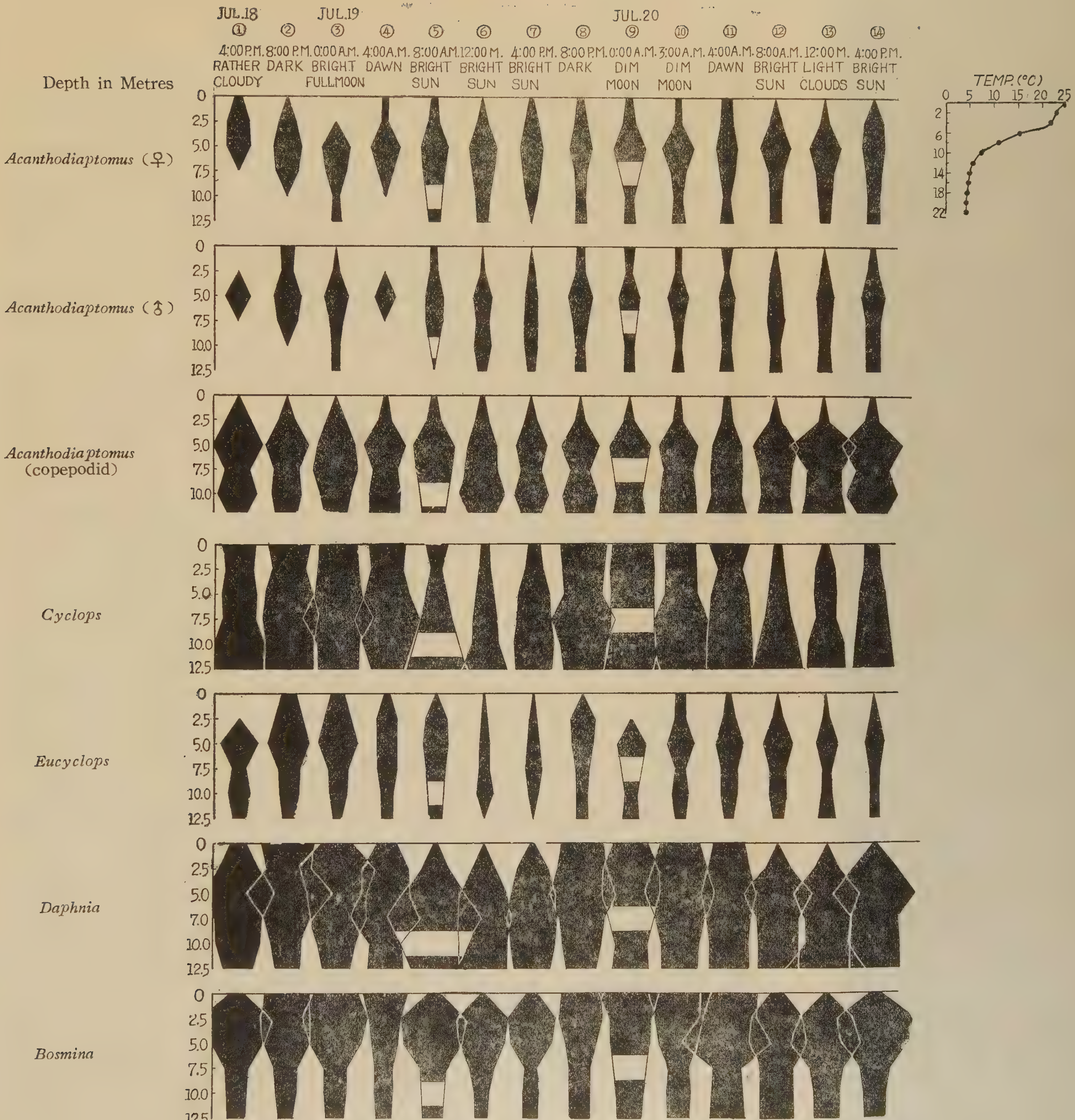


Fig. 9. Diurnal migration of plankton crustaceans in July 18th—20th, 1943, in Lake Tsugarujuni (Observation 9)

at the surface at 4:00 p. m. on the 18th, while the number at the surface greatly increased at 8:00 p. m., the maximum layer remaining still at the 5 metre depth. The number at the surface slightly decreased under the moon at 0:00 a. m. on the 19th. However, the maximum layer existed at 2.5 metres, the animals having ascended from the deep. At 4:00 a. m. on the 19th the number at the surface became less and the maximum layer sank to 7.5 metres, the number there becoming larger at 8:00 a. m. The animals remaining at the surface were very few during daylight until 4:00 p. m., but the ascending tendency was clearly shown by the increasing number at 2.5 metres from noon to 4:00 p. m. At 8:00 p. m. the animals again appeared very abundantly at the surface, though a considerable number of them still remained in the lower layers. The distribution at 0:00 a. m., 3:00 a. m. and 4:00 a. m. on the 20th was nearly similar with that at 8:00 p. m. on the 19th. The number at the surface and 2.5 metres again decreased at 8:00 a. m., while that at 5 metres increased. During the hours from noon to 4:00 p. m. on the 20th the number at 2.5 metres increased by about six times. From the above results it is noticed that *Daphnia* was making clear vertical migration passing through the thermocline. However, so far as the results obtained on the 20th are concerned, the number of animals below the thermocline was nearly constant through all day. Ascending movement did not take place until 4:00 p. m., but it finished before 8:00 p. m. At night the animals were nearly uniformly distributed from the surface to 12.5 metres. Descending movement began at about 4:00 a. m. and was completed by 8:00 a. m.

The vertical migratory movement of *Bosmina longirostris* was almost limited to the layers above the thermocline, the number of animals below the thermocline not varying throughout the day and night. The animals were concentrated in the maximum number at 2.5 metres at 4:00 p. m. on the 18th, and in a considerable number at the surface. Ascending movement was accelerated until 8:00 p. m., the number at the surface becoming thirty-fold. Then above 5 metres they became nearly uniform in vertical distribution. Some of the animals descended to 2.5 metres from the surface at 0:00 a. m. on the 19th, probably affected by the moonlight, while they ascended again at 4:00 a. m., getting the maximum number at the surface. The number at the surface decreased to one thirtyth of that four hours earlier and the majority of the animals were distributed in 2.5 5 metres at 8:00 a. m. The animals were very few at the surface at noon, majority being in 2.5 5 metres, but the number at the surface increased eight-fold at 4:00 p. m. Ascending migration had finished by 8:00 p. m., and the number found from the surface to 2.5 metres greatly increased. At 0:00 a. m. on the 20th under the weak light of the moon, the maximum layer was seen at the surface. The number at the surface increased at 3:00 a. m. The maximum layer descended to 5 metres at 4:00 a. m., though a large number still remained at the surface. The number at the surface decreased to one one-hundredth at 8:00 a. m., with the decrease continuing until noon. The animals again ascended at 4:00 p. m., the number at the surface becoming about nine times as great. Thus, the descending migration of this species took place during the hours from midnight to 4:00 a. m., while the ascending

movement occurred during the time from 4:00 a. m. to 8:00 p. m.

Together with the above five species, a cladoceran, *Scapholeberis mucronata*, and a copepod, *Canthocamptus staphylinus* were also collected, though the number was very small.

(4) Summary of Observations on Diurnal Migration

(a) Female of *Acanthodiaptomus yamanacensis*

In Lake Shikotsu in summer, the animals were distributed nearly uniformly throughout all depths at midnight (Fig. 7, ①, ②). Descending from the surface took place at about 2:00 a. m. (Fig. 7, ③). When the weather was fine, the animals almost disappeared from the surface after dawn at about 5:00 a. m. (Fig. 7, ⑤). The number of the animals in lower layers increased as the sun rose high (Fig. 7, ⑦ ⑫), while the animals were very few above 5 metre depth after about 10:00 a. m. (Fig. 7, ⑩) and above 10 metres at noon (Fig. 7, ⑫). They were distributed frequently below 15 metres to about 40 or 50 metre depth, and decreased below that, some having been found even at 95 metres at midday (Fig. 2). Ascending migration had already begun before 1:00 p. m. and the number at 5 metres somewhat increased at this time (Fig. 7, ⑬). Then ascending movement was accelerated until the maximum layer rose to 5 metres and a certain number appeared at the surface at 7:00 p. m. (Fig. 7, ⑲). The number at 5 metres became extraordinarily large just after the dusk of the evening, i. e. at about 7:00-8:00 p. m. (Fig. 7, ⑲, ⑳). The distribution became again nearly uniform after 9:00 p. m. and this condition was maintained until midnight (Fig. 7, ㉑-㉓). The animals were distributed at shallow depths in the cloudy weather as compared with the fine (Fig. 7, ⑯ ⑱, ㉖, ㉗, but ㉔ and ㉕ are different). The vertical distribution at 5:00 p. m. in October, when the daytime was short and it became dusk at this hour, was nearly uniform (Fig. 8, ①), though the animals disappeared from the surface at this time in summer even under heavy clouds (Fig. 7, ⑱). At 4:00 p. m. in summer under heavy clouds the animals were found at the surface, though rather rarely (Fig. 7, ⑰). The number at the surface increased in darkness at 6:00 p. m. in October (Fig. 8, ②). They were distributed frequently at the surface at dawn at 6:00 a. m. (Fig. 8, ③) and still continued a uniform distribution even under the bright sun at 7:00 a. m. in October (Fig. 8, ④). On the contrary, the animals had already become rare in 0-5 metres and most of them had descended below 10 metres in summer at this hour (Fig. 7, ⑦). The number at the surface decreased at 8:00 a. m. in October (Fig. 8, ⑤) and the maximum layer sank down to 15 metres at 10:00 a. m. under the bright sunshine (Fig. 8, ⑥). In comparing the above with the distribution in summer (Fig. 7, ⑧, ⑩) it is clear that the animals were found in deeper layers in August than in October. The altitude of the sun was about 19° at 8:00 a. m. and about 32° at 10:00 a. m. in October, while it was about 35° and 55° respectively in August. Thus it is obvious that the animals migrated upward and downward in correlation with the change of light intensity.

In Koikuchinoike of the Tsugarujuni Lake Group the females of *Acanthodiaptomus* abundantly occurred in 2.5 5.0 metre depth and also considerably at the surface at 4:00 p. m. in cloudy weather (Fig. 9, ①), while the maximum distribution existed in 10-15 metres under the similar conditions at Lake Shikotsu (Fig. 7, ⑰). In darkness at 8:00 p. m. the maximum distribution in both lakes was kept at 5 metres (Fig. 9, ②, ⑧, Fig. 7, ⑳). The maximum layer at midnight under the moonlight existed at 5 metres at Lake Tsugarujuni (Fig. 9, ③, ⑨), while at Lake Shikotsu it was at 15 metres (Fig. 7, ①). The maximum layer at 4:00 a. m. at Lake Tsugarujuni was at 5 metres (Fig. 9, ④, ⑪) and at 10 metres at Lake Shikotsu (Fig. 7, ④). The maximum layer at 8:00 a. m. at the former lake was also at 5 metres (Fig. 9, ⑤, ⑫), while the greatest concentration of animals was seen in 10 20 metres at Lake Shikotsu (Fig. 7, ⑧). At noon the animals avoided the surface layer at both lakes, the maximum distribution being found at 5 metres at Lake Tsugarujuni (Fig. 9, ⑥, ⑫), but they crowded in 15 20 metre depth, having almost disappeared above 10 metres at Lake Shikotsu (Fig. 7, ⑫). The difference of the vertical distribution between the two lakes is caused by the difference of transparency of water which was 5.5 metres at Lake Tsugarujuni and 16 metres at Lake Shikotsu, that is, in turn, the difference of the light intensity in the water.

(b) Male of *Acanthodiaptomus yamanacensis*

In Lake Shikotsu the stratification of the males of *Acanthodiaptomus* was more distinct than in the females (Fig. 7). The males were distributed in a considerable number in upper layers, rather decreasing in lower, during night, while the females kept a uniform distribution at night. The large population of males was found in the deeper layers as compared with the females under the bright sun. Moreover, the males had a strong tendency to migrate upward when the sun was covered with thick clouds (Fig. 7, ⑱, ㉔, ㉕, but ⑰, ㉗). The number of males which left the surface when the moon began to shine was larger than that of the females (Fig. 5, ③). The crowding of the males at about 15 metres was very remarkable in daytime (Fig. 2). The number was very large in shallow layers at dusk and at darkness just after dusk in October (Fig. 8, ①, ②). However, this type of distribution was not to be found at dawn, the animals being distributed almost uniformly (Fig. 8, ③). They avoided the sun light in autumn and in summer as well (Fig. 8, ⑤, ⑥). A considerable number of the males still remained in upper layers under the bright sun even one hour after daybreak in autumn as did the females (Fig. 8, ④). The vertical distribution in fine weather differed from that in cloudy weather in autumn as in summer (Fig. 3). Comparing the vertical distribution at Lake Tsugarujuni in summer with that at Lake Shikotsu, the males were also distributed in shallower layers at the former lake like the females (Fig. 9). The males were regarded to be more sensitive to the light than the females, the males more remarkably migrating with the change of light intensity.

(c) Copepodid of *Acanthodiaptomus yamanacensis*

The copepodids had a tendency to remain in the shallow layers as compared with the adults, though they did also a diurnal migration similar to that of the adults (Fig. 2, 7). The morning downward migration began at about 6:00 a. m. and the upward in the evening was completed before 5:00 p. m. at Lake Shikotsu in summer (Fig. 7, ⑥, ⑰). The animals were concentrated in the shallow layers at night, decreasing in number below 10 15 metres (Fig. 6, ⑨, Fig. 7, ①-③, ⑳-㉓). We had generally a bright sky with the sun hanging high at 6:00 p. m. in late June, the sun being in the solstitial point, while it was twilight at this time in August. Neverthless, the distribution of the animals in both cases did not differ much, both showing crowding at high levels (Fig. 4, ⑧ including adults, Fig. 6, ②). Moreover, the distribution was nearly the same at 6:00 a. m. both in June and August, though the sun was higher in the sky in June than in August (Fig. 6, ③, Fig. 7, ⑥). In addition, the maximum layer existed in shallower layer in June than in August at 8:00 a. m., 10:00 a. m. and at noon under the bright sun (Fig. 6, ⑪-⑬, Fig. 7, ⑧, ⑩, ⑫). Again ascending migration under heavy clouds was accelerated in June (Fig. 6, ⑥, ⑦). The copepodids occurring in August were in more advanced developmental stage than in June, and they possibly became sensitive to the light as they developed further.

The copepodids at Lake Tsugarujuni hardly occurred at the surface throughout the day even in dark night (Fig. 9). The range of the diurnal migration at Lake Tsugarujuni was less than at Lake Shikotsu. Below 5 metres the copepodids remained nearly in constant number throughout the day as did the adults.

(d) *Daphnia longispina* subsp. *hyalina*

The specimens of *Daphnia longispina* subsp. *hyalina* collected in June, August and October at Lake Shikotsu included animals in various stages with different body length, which had developed from parthenogenetic eggs.

Downward migration in the morning took place during the period 6:00-8:00 a. m. at Lake Shikotsu both in June (Fig. 6, ③, ④, ⑩, ⑪) and August (Fig. 7, ⑥-⑧), and the same was observed in October (Fig. 8, ③-⑤). Upward migration in the evening began before 6:00 p. m., some of the animals appearing at the surface, when the sun was still bright in June (Fig. 6, ②). Similar distribution was also observed at the same hour in darkness in October (Fig. 8, ②). The animals were found abundantly in the deeper layers in both cases. At night the animals occurred at 5 metres or the surface in a large number and also considerably in lower layers in June (Fig. 6, ⑨). However, they crowded in the lower layers, though some of them remained at the surface, in August (Fig. 7, ①-③, ⑳-㉓). The present subspecies known as the cold water form might escape from 0 5 metre depth in August, as the surface temperature rose to 21.5°C with the thermocline at the 10 15 metre depth. The tendency of the higher distribution

under heavy clouds was observed both in June (Fig. 6, ⑥, ⑦, ⑧), in August (Fig. 7, ⑯ ⑱, ㉔-㉗) and in October (Fig. 3).

(e) *Daphnia longispina* subsp. *longispina*

The subspecies *longispina* distributed in Lake Tsugarujuni is considered as the warm water form. It was collected from 2.5 metres in some number and in great number below 5 metres, with the maximum at 7.5 metres, at noon under the bright sun at Lake Tsugarujuni (Fig. 9, ⑥). The animals were found in very shallow layers as compared with other subspecies, *hyalina*, at Lake Shikotsu (Fig. 7, ⑫). The reaction to the moonlight was also observed; for instance, when there was a bright full moon (age 17 days), many animals descended from the surface to 2.5 metre layer, while they did so only a little under the moon covered with clouds (Fig. 9, ③, ⑨). Under the cloudy weather at 4:00 p. m. the maximum layer of subsp. *longispina* at Lake Tsugarujuni was shallower by more than 15 metres than that of subsp. *hyalina* at Lake Shikotsu (Fig. 7, ⑰, Fig. 9, ①). Although the above difference of the vertical distribution between two subspecies may come from the varying degrees of transparency of water of the lakes, the difference of distribution at night cannot be ascribed to the light condition. In darkness at 8:00 p. m. subsp. *longispina* was distributed at 5 metres in the maximum number and also abundantly at the surface where the temperature was above 22°C at Lake Tsugarujuni (Fig. 9, ②,⑧), while the other subspecies, *hyalina*, at Lake Shikotsu showed the maximum distribution at 15 metres, with comparatively rare distribution at the surface at 8:00 p. m. and 9:00 p. m. (Fig. 7, ⑳, ㉑). The subspecies *hyalina* disliked the warm water (above 20°C) in the epilimnion.

(f) *Scapholeberis mucronata*

The present species was found very commonly in the surface water almost the whole day and night in the summer of 1942 at Lake Shikotsu (Fig. 4), but the number was comparatively poor in other collections. Differing from other species, *Scapholeberis* did not dislike the bright sun light at the surface.

(g) *Bosmina coregoni*

This species was collected in October, 1946, at Lake Shikotsu. The maximum distribution was found at 20 25 metre depth around noon under the bright sun. However when the weather was cloudy the animals tended to make some upward movement (Fig. 3).

(h) *Bosmina longirostris*

The present species was collected abundantly in summer at Lake Tsugarujuni. The maximum layer at noon under the bright sun was found at 2.5-5 metres (Fig. 9, ⑥, ⑬),

the animals having invaded into the warm water of epilimnion. At Lake Shikotsu another species, *Bosmina coregoni*, was frequented in the metalimnion, being rare in the upper warm water. *Bosmina longirostris* occurred usually in the maximum number at the surface in darkness or under the dim moonlight at Lake Tsugarujuni (Fig. 9, ②, ⑧-⑩). The vertical migration of this species in summer at Lake Tsugarujuni was limited to the layers above the metalimnion, and some individuals distributed below this level did not make conspicuous migration, remaining stationary throughout day and night.

(i) *Cyclops strenuus*

Cyclops strenuus was migrating up and down passing through the thermocline at Lake Tsugarujuni. The number of individuals increased with depth, exhibiting the maximum occurrence below 12.5 metres in daytime (Fig. 9, ⑤, ⑥, ⑫, ⑬). However, the distribution was nearly uniform in any layer at night, though the largest number was found in most cases at 7.5 metres (Fig. 9, ②, ③, ⑧, ⑨). Apparent descent took place at 4:00 a. m. after dawn (Fig. 9, ④, ⑪), and ascent began at about 4:00 p. m. under the bright sun (Fig. 9, ①, ⑦, ⑭).

(j) *Eucyclops prasinus*

The number of animals collected was scant in the observation at Lake Tsugarujuni. The animals withdrew from the surface and were distributed most frequently at 5 metres in daytime in most cases (Fig. 9, ①, ⑤-⑦, ⑫-⑭), while their maximum layer was found at 2.5 or 5 metres during the night. Some of the animals still remained at the surface at 4:00 a. m. at dawn (Fig. 9, ④, ⑪). In this species the migration through the thermocline was not remarkable.

VII. Experiments on Photo- and Geotropism

The experiments on the photo- and geotropism of plankton animals were carried out on October 18th to 20th, 1946, (two supplementary experiments on July 5 th, 1948) at Lake Shikotsu, and some additional experiments were made a few days after at Sapporo using the materials brought from the lake. The materials collected at Lake Shikotsu in this season included four species, viz., *Acanthodiaptomus yamanacensis*, *Daphnia longispina* subsp. *hyalina*, *Scapholeberis mucronata* and *Bosmina coregoni*. The experiments were arranged in three series: (1) geotropism in diffuse light, (2) geotroism in darkness and (3) phototropism. Besides them, the reaction of the animals in the vertical glass tube when the light was given from above or from below was observed, and next the glass tube was put vertically in the lake and the movement of the animals in it was observed.

The apparatus used in the experiments was a glass tube, 3.5 cm in diameter and 60 cm

in length, with three marks dividing it into four sections (Fig. 10). Both ends were plugged with cork stoppers which were pierced by thin glass tubes. The rubber tubes connected with glass tubes were gripped with pinch corks. The glass tube was filled with water including test animals which were obtained by net haul extending to the 15 metre depth. Before bringing into the experiments, the animals were kept in a vessel with cover suspended in the surface water of the lake for a certain time. The determination of the grade of reaction was made by calculating the number of individuals distributed in four sections for each species after exposure to the experimental conditions.



Fig. 10 Glass tube for experiments on tropism of plankton animals.

When the exposure was finished, the glass tube was kept vertically and the upper pinch cork was removed. Then the water in the lowest section containing samples was flowed into a sample bottle by loosening the lower pinch cork. Thus the water containing the materials of each section, i. e. IV, III, II and I, of the glass tube was transferred into separate sample bottles. With these samples an identification of the separate species and calculation of number of individuals were made by the aid of binocular microscope. Of *Acanthodiaptomus* the number of the females and the males was counted respectively. Before pouring water containing samples into the glass tube at the beginning of the experiment, the temperature of the water was measured, and just after transferring into the sample bottles final temperature was also recorded. In the experiments made in October the initial temperatures varied from 11.3 to 13.2°C and the final temperatures from 11.2 to 13.5°C. The air temperature in daytime in this season was about 10 to 13°C and that of the surface water of the lake was 13 to 14°C, being nearly equal to that of the air. It hardly varied until at a depth of 15 metres.

(1) Geotropism in Diffuse Light (Exps. 1-4, Table 10)

The glass tube was stood vertically with section I up and exposed in diffuse light indoors so that every part of the glass tube, from the top to the bottom, received the diffuse light in equal intensity (Fig. 11, A).

In Exp. 1 the female *Acanthodiaptomus* showed obvious upward movement after exposure to the diffuse light for one hour; that is, it is negatively geotropic in diffuse light. Exp. 2 also indicated that the females were negatively geotropic in diffuse light, though the largest number was seen in section II. This tendency was also found after exposure for 30 minutes (Exp. 3). The males were also negatively geotropic in diffuse light, more distinctly than the females (Exps. 1-3).

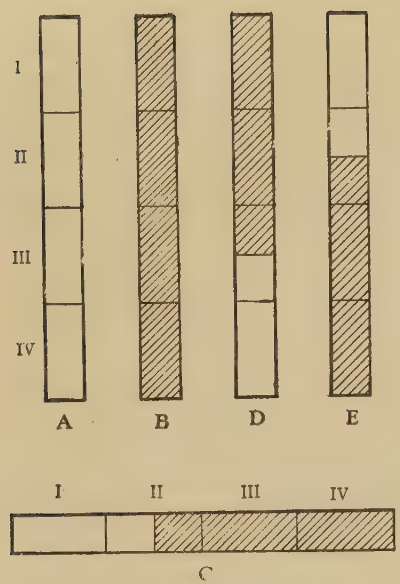


Fig. 11 Various conditions of experiments. [hatched] indicates portion of tube covered with black paper.
A. For geotropism in diffuse ligt
B. For geotropism in darkness
C. For phototropism
D. Light given from below
E. Light given from above

Daphnia had a remarkable tendency of positive geotropic migration in diffuse light (Exps. 1-3), but *Scapholeberis* was distinctly negative geotropic (Exp. 4). In *Bosmina* the result of Exp. 1 showed somewhat positively geotropic movement.

(2) Geotropism in Darkness (Exps. 5 8, Table 11)

The experiments on geotropism in darkness were made using the glass tube covered with a thick black paper (Fig. 11, B). As soon as the experiment was accomplished, the black cover was removed and the samples were quickly poured down into the separate bottles. It was shown that in Exp. 5 some individual animals were found to become inactive during the experiment and were deposited on the underside cork. These might be counted together with those actively swimming animals in section IV (undermost section) and therefore consideration would be sections I-III, ommitting section IV.

The females of *Acanthodiaptomus* in Exp. 5 were neither positively geotropic nor negatively, the largest number being in section II. Exp. 6 also yielded uncertain results in respect to the particular reaction to gravity. This was likewise the case in Exp. 7. The males also showed rather neutral geotropic reaction in darkness (Exps. 5 7) as did the females.

Daphnia was very slightly negative geotropic in Exp. 5 and the same tendency was also seen in Exp. 6 in which, however, the largest number was in section IV. In Exp. 7 the animals moved as positively in response to gravity. But these tendencies, either negatively or positively geotropic, were very slight, and so the present species might be neutral geotropic in darkness in general.

The geotropic reaction of *Scapholeberis* in darkness was not characterized in Exp. 6, but when section IV was excluded, it was evidently negative. In Exp. 8 the negative geotropism of this species in darkness was distinct. *Bosmina* was slightly negative geotropic in darkness (Exp. 6).

(3) Phototropism (Exps. 9-11, Table 12)

The experiments were done with a glass tube, which was laid horizontally. A part of the glass tube was wrapped with a black paper, covering a half of section II and all of

sections III and IV, while section I and a half of section II were not screened (Fig. 11, C).

In Exp. 9 the exposure was made near the window in the laboratory in the afternoon of a rainy day. The maximum number of females of *Acanthodiaptomus* was found in section II after exposure for one hour. Thus, it was indicated that the animals were attracted to the boundary zone of light and shadow, that is, to rather faint light. Exp. 10 was made by suspending the glass tube horizontally in the surface water of the lake under the bright sun. Even after 30 minutes exposure the animals crowded in the brightest section. The number of animals in sections II and III diminished in order and there was no animal in section IV. Exp. 11 was made in the dim light in the laboratory at dusk. The exposure lasted from 4:45 p. m. to 5:15 p. m. The result after the 30 minute exposure showed the maximum distribution of the female *Acanthodiaptomus* in section II. The males of *Acanthodiaptomus* showed similar reaction in these experiments, namely positively phototropic.

Daphnia also made positively phototropic movement in these experiments, the largest number being found always in section II, the bounary section between light and shadow. The positive phototropism of *Scapholeberis* was most conspicuously indicated among the four species (Exps 9, 10). Next came that of *Bosmina* of which the largest number was always in section I, the brightest section. The above described experiments indicated that the phototropic reaction was most intensive in *Scapholeberis*, becoming less in *Bosmina*, *Acanthodiaptomus* and *Daphnia* in order.

(5) Migration in Light Given from Below (Exp. 12, Table 13)

The present experiment was attempted to observe the combined effect of geotropism and phototropism of the animals on their movement. The glass tube was wrapped with black paper except a half part of section III and the whole of section IV. In vertical position with section I up, the tube received the light only at the lower part (Fig. 11, D). The experiment was made by exposing the glass tube to diffuse light indoors for one hour.

The females of *Acanthodiaptomus* were distributed in largest number in section IV, the brightest section. According to the previous experiments the females were slightly negative geotropic in diffuse light, neutral geotropic in darkness and positively phototropic to light. So the distribution in this vertical glass tube lighted in the lower part would indicate that the phototropic movement overcame the negative geotropic movement. The downward migration of the males was somewhat indistinct as compared with that of the females; this agreed with the result of experiment in diffuse light that the negative geotropic reaction of the males was more intensive than that of the females.

The downward migration of *Daphnia* was strongly marked. It was natural for this species was strongly positive geotropic in diffuse light, nearly neutral geotropic in darkness and phototropic to light. *Bosmina* was highly phototropic, and the result of the present experiment showed that this species was most abundant in section IV and the

number diminished upward in order. However, this tendency was not distinct as compared with other species, probably due to the negative geotropism in darkness.

(6) Migration in Light Given from Above (Exp. 13, Table 14)

Differently from Exp. 12, the lower five-eighths of the glass tube was wrapped with black paper, the upper three-eighths remaining uncoverd (Fig. 11, E).

In this experiment all forms except the males of *Acanthodiaptomus* made downward movement, but the movement was in less degree than was observed in Exp. 12. The phototropic reaction probably checked the downward movement. The downward migration was most remarkable in *Daphnia*, this agreeing with the earlier finding that its geotropism was strongly positive in diffuse light.

(7) Photo- and Geotropism in Relation to Vertical Distribution in Nature

From the results of the above experiments the grade of phototropic reaction and geotropic reaction in diffuse light and darkness in five forms of plankton crustaceans may be compared as in the following table:

	phototropism	geotropism	
		in diffuse light	in darkness
Acanthodiaptomus yamanacensis ♀	+ +	−	N
Acanthodiaptomus yamanacensis ♂	+ +	− −	N
Daphnia longispina subsp. *hyalina*	+	+ +	−, N, +,
Scapholeberis mucronata	+ + + +	− −	− −
Bosmina coregoni	+ + +	+	−

+ : positive − : negative N : neutral

It is of interest that these tendencies be considered in relation to the actual vertical distribution at Lake Shikotsu. The vertical distribution in daytime in fine weather is taken to be that obtained in October, 1946 (Fig. 3). The maximum number of all species, excepting *Scapholeberis* was found at a considerable depth under the surface, but Exp. 10 indicated that each species except *Daphnia* was most abundant in section I which was exposed to bright sun. The behaviour of animals was different in the test tube from that in nature. Fig. 3 shows that the vertical distribution of the females of *Acanthodiaptomus* was somewhat deeper than that of the males. This agreed with the result of laboratory experiment that the negative geotropic reaction of the males in diffuse light was more intense than in the females. *Daphnia* was distributed at slightly deeper layers than *Acanthodiaptomus* in the lake. According to the laboratory experiments, phototropic reaction of *Daphnia* was weaker than that of *Acanthodiaptomus*, while geotropic reaction in diffuse

light was strongly positive in *Daphnia*. The laboratory experiments had shown that positive phototropic reaction of *Bosmina* was stronger than that of *Daphnia*, but positive geotropic reaction of the former in diffuse light was weaker than that of the latter. From this, the vertical distribution of *Daphnia* should be lower than that *Bosmina*. Neverthless, the maximum distribution of both species was found at the same depth (20m). It was perceived, however, that the number of *Daphnia* was larger in the deeper layers than that of *Bosmina*. *Scapholeberis* was abundantly distributed at the surface and near by. This was quite natural because this species was very intensively positive phototropic toward the light and strongly negative geotropic in diffuse light. For the vertical distribution in the lake at night the results in summer of 1943 and 1944 (Figs. 5, 7) are taken. Generally the difference of number between upper and lower layers was small in *Acanthodiaptomus*. The neutral geotropism in darkness of this species might induce the nearly uniform vertical distribution at night. *Daphnia* occurred abundantly in 10 20 metre depth at night, but it was rare above 5 metres. The scarcity in the epilimnion was probably induced by the high temperature there. The neutral, sometimes positive or negative, geotropic reaction of *Daphnia* in darkness might force uniform distribution under the epilimnion. *Scapholeberis* was distributed in the shallow layers at night as well as in the daytime. In laboratory experiment its geotropism in darkness was very negative.

(8) Migration in Vertical Glass Tube Suspended in Water (Exps. 14-18, Table 15)

The experiments were made in the water of Lake Shikotsu (Exps. 14 16) and in a pond at Sapporo (Exps. 17, 18) both under the bright sun. The glass tube was suspended in the water vertically; section I was the uppermost and the section IV was the lowest. The top of the glass tube was uncovered when the experiment was made at the surface water, but in the experiment under the surface the top was covered with a small transparent glass disk. The five experiments were made at different depths, viz., 0 m (twice), 1m, 2 m and 5 m depths. Exps. 14 and 18 which were made at the surface of water showed that the females of *Acanthodiaptomus* always moved down, but the males preferred section II in Exp. 18. The number of the females was largest in section III at 1 metre depth, while the males were most abundant in section II and the number in section I was also large (Exp. 17). At 2 metre depth the largest number of the females was in section II, and that of the males in section I (Exp. 16). This was also the case for 5 metre depth (Exp. 15). Thus the downward movement of *Acanthodiaptomus* was indicated to be lessened with increasing depth, moreover, the males showed a greater tendency of upward movement than did the females. The laboratory experiment above described indicated that the negative geotropic reaction was more intensive in the males than in the females. It was noticed that both the females and males have tended to move up even at a few metre depth in spite of the fact that they were very rare above 5 metres in the lake in fine weather. The space effect by capturing the animals in the narrow glass tube might produce the different behaviour of the animals. They became less sensitive to the

stimulation of the sun light. *Daphnia* always moved down when laid in the glass tube suspended at depths below the surface to 5 metres (Exps. 14-18). However, as might be expected, the tendency of downward movement became indistinct with increasing depth. The geotropic reaction of *Daphnia* in diffuse light was strongly positive, differing from *Acanthodiaptomus*, in the laboratory experiment. It was natural that the former showed a more indistinct tendency of upward movement in the test glass tube (Exps. 14-18) than did *Acanthodiaptomus*.

VIII. Discussion

Forel (1876) explained that plankton animals sink in daytime with the sinking water mass, of which the movement is caused by wind blowing towards the shore from off, and the animals appear near the surface with upwelling water at night, when the wind blows conversely. Ostwald (1902, 1903) regarded that the diurnal migration is largely due to alternations of viscosity of the water, which in turn varies with the temperature. However, he thought that this is not the only influence, but that the tropism of animals plays a part.

Franz (1910, 1911, 1912, 1913) insisted that the animals are really abundant at the surface during day and night, but they escape the net when it is light enough for them to see. Southern and Gardiner (1926) believed also that the difference of plankton number in collections by day and night is due to their ability to see and aviod the net. In some large plankton animals, e. g. euphausiids, which are strong swimmers this may be true, but in the present investigation on copepods and cladocerans this surely was not the case.

Ewald (1910, 1912), who made laboratory experiments with cladocerans and the larvae of barnacles, held the view that if the light is too intense, the animals cease their movement and so sink, and when they reach a region with lower intensity of light, they recover the swimming movement again. Accordingly, the animals remain in the region in balanced condition of illumination all day long.

It has been said that certain plankton animals, such as cladocerans, do not swim directly in a vertical direction in the diurnal movement, but, instead, arrive at their destinations by a diagonal path. Bainbridge (1952) made an interesting observation on the swimming of marine zooplankton by diving underwater himself. He stated that the diurnal vertical migration of *Calanus finmarchicus* is a direct and straight swimming up or down through the water column, and not the result of random movements. The author made an observation on the movement of marine copepods in the deep by the aid of under-sea observation chamber "Kuroshio" (Inoue, Sasaki and Oaki, 1952, 1953). The copepods captured in glass cylinder, in which the water received the pressure in the depth by means of rubber tubing, showed a tendency of straight advance upward during the sinking, i. e. with increase of the pressure, to the depth of about 100 metres. Hardy and Paton (1947) supposed that the plankton makes a vertical movement by the aid of a sense

of depth, and Hardy and Bainbridge (1951a) experimented that decapod larvae move upward when laid under the increasing pressure.

The theory that the metabolic rhythm of animals causes the periodical upward and downward movement was proposed by Menke (1911) and was partly supported by Loeb (1914). Esterly (1919) believed also the metabolic rhythm is related to the diurnal movement of marine copepods. According to the recent opinion, the causative factors for the diurnal movement of plankton animals are found in the environment but not in the organisms themselves. As Welch (1935, p. 234) stated, physiological rhythm possibly occurs to some extent in certain plankton animals, but such rhythm may be merely a reflection of the periodic changes of the environment and should be regarded as a result rather than cause.

The external factors which govern the diurnal migration of plankton seem to be mainly light, gravity, temperature and so on. Weismann (1877) and Fuchs (1882) stated that crustaceans like faint light, making diurnal migration with the change of light intensities. Groom and Loeb (1890), Parker (1902), Rose (1925) and Kikuchi (1938) proved experimentally on various species of animals that the phototropism of animals varies with the change of the intensity of light and consequently animals retain the level with the optimum intensity of light. Russell (1927a, 1934), Clarke (1933, 1934) and Kikuchi (1937) also affirmed that fact from field observations. According to Waterman and his coworkers (1939), a considerable part of the migrations of deep-water molacostracan crustaceans takes place while the light intensity even at the surface was no greater than star light. They concluded that at some time of day the bathypelagic organisms concerned are affected by light penetrating into deep layer from the surface.

Ishida (1936), experimenting on barnacle nauplii, noticed that the reaction to light is different with individuals, some of them swimming toward light (skotophobic), while some others swimming from it (photophobic). Johnson (1938) experimented on the phototropic movement of *Acartia clausi*, and reported that decrease in light intensity forces the animals to migrate upward, and the greater the change in light, the greater the upward movement. Furthermore, he said that the animals are not seeking an optimum intensity since their distribution become uniform when left for some time under the intensity in which they first moved upward. It is of importance whether the animals react to the change of intensity of light or to absolute magnitude of the light intensity. The recent opinion tends to the belief that the animals react to the change of intensity of light, but have no relation to the absolute magnitude of intensity.

The animals are said to be usually desirous of escaping from the direct sun rays. According to the experiment made by Lepeschkin (1931), some marine copepods after exposure to direct sun light become less resistant to poisons which were added to the water. He remarked that the ultraviolet rays in the sun light have an effect of diminishing the harmful effect of visible rays of the sun light. Marshall, Nicholls and Orr (1935) observed that the oxygen consumption by respiration of *Calanus finmarchicus* under bright

diffuse light or sun shine becomes twice as great in darkness. Thus, it seems the strong sun light has an injurious effect on plankton animals. It is natural that the animals move down in deeper water during a bright sunny day. Concerning the reaction of the animals to ultraviolet rays, Loeb (1906) made an experiment in which the animals were found to be negative in tropism when exposed. Mori (1935) found by experiment that the daphnid, *Moina macrocopa*, is most attracted by the blue indigo rays of the spectrum.

The diurnal migration of *Acanthodiaptomus yamanacensis* in Lake Shikotsu has been reported already by Kokubo (Tanakadate, 1925), Hayashi and Natori (1932) and the present author (1934). They held the view that the animals migrate upward and downward with the change of light intensities. In the present investigation in Lake Shikotsu all species except *Scapholeberis mucronata* manifest diurnal migration periodically with the change of light condition and in Lake Tsugarujuni too. Downward movement under the bright moon light is also observed in various species. The type of vertical distribution in fine weather is distinctly different from that in cloudy weather in daytime in the same lake. Furthermore, all animals except copepodids of *Acanthodiaptomus* are found in shallow layer in daytime at Lake Tsugarujuni, in which the water is less transparent, that is, more scanty of under-water illumination. These facts force one to the conclusion that the change of light intensity under water governs most effectively the diurnal movement of plankton. The relation of the vertical distribution of animals to the intensity of light is also valid in the seasonal difference of vertical distriburion of adult *Acanthodiaptomus* as observed in August and October at Lake Shikotsu. However, the animals begin to leave the surface at about 2:00 a. m. in perfect darkness (p. 26); the factor governing the descending movement at this time is not the light.

The "twilight migration" is a movement in which the plankton animals move up near the surface at dawn and evening twilight, descending both in daytime and midnight. This was reported by Kikuchi (1930a) on *Cyclops strenuus*, nauplii of copepods, *Bosminopsis deitersi* and *Polyphemus pediculus* at Lake Kizaki. In the present investigation this type of migration was not apparent, except for one example of adult *Acanthodiaptomus*. *Acanthodiaptomus*, especially adult males, show upper crowding in vertical distribution in the evening dusk and following darkness, and then the distridution becomes gradually uniform through vertical range with the lapse of time. Such remarkable ascending movement in the evening was indicated also by Farran (1947) on the adult males of *Calanus finmarchicus* off the south coast of Ireland. In darkness, the animals which are neutral geotropic are scattered and distributed nearly uniformly, free from any stimulation of light. The upward movement at dawn was not observed in the present investigation. It may be supposed as the authors (Motoda and Ishida, 1950) mentioned that the animals move up in the evening twilight because their negative geotropic movement is produced when they are just freed from the stimulation of strong day light, while at dawn they do not move upward to the surface because the conditions are the reverse.

It has been reported that certain plankton animals adapt themselves to go to light and

come to endure the comparatively strong light, after being exposed for certain hours. Some authors stated that the animals are often found to frequent a higher level at midday, subjected to high irradiation than in early morning. Southern and Gardiner (1932), Clarke (1934a), Harada (1934), Kikuchi (1937) and Motoda and Ishida (1950) have reported such examples. However, this was not noticed in the present observation.

It has been often observed that the ascending animals are found in the evening in lower layers than the layer of optimum light intensity for the animals. In this case ascending animals may delay in reaching the layer of optimum light. However, at dawn descending animals swim down quickly following the optimum light. Thus, as mentioned by Clarke (1934a) on *Calanus finmarchicus* in the Gulf of Maine, for the animals which move upward in the evening covering more than 100 metres, the speed and the duration of the swimming movement serve as important factors controlling the vertical distribution. According to Waterman and his coworkers (1939), the speed of vertical movement in diurnal migration varies from 24 to 125 metres per hour among the deep-water molacostracan crustaceans. Moore (1949) indicated that the copepod, *Pleuromamma abdominalis*, can ascend at a rate of more than a metre per minute. Hardy and Bainbridge (1951b) stated that *Calanus finmarchicus* is able to ascend 50 feet in one hour, and *Meganyctiphanes* can ascend as much 305 feet in the same time. It has been said that swimming speed of plankton animals varies with varying light intensities and the animals in full darkness move at minimal speeds or not at all (Cushing, 1951, pp. 184 187). In the present investigation the range of vertical movement is confined to a comparatively short distance; the time required for changing the vertical distribution of the animals is in fact not an important factor.

Franz (1913) suggested that animals in the water may be stimulated by light from all sides, even from beneath, by the diffusion of light, except when they are close to the surface or to the bottom. Esterly (1919) stated that animals when at a depth of one hundred feet might not be aware of the light direction, as the light is so much diffused. Kikuchi (1938) measuring under-water illumination at Lake Kizaki by means of photoelectric cell, found that at 10 metre depth the illumination from above was 13 % of that just below the surface and the horizontal light intensity was about 9 %, while the light from below was only 0.9 %. The transparency of this lake in summer was measured as about 5 metres (Kikuchi, 1937). On the diffusion of light in sea water, Takenouchi (1949) made an experiment, and stated that an erroneous conception about diffused light in sea water still remains, that the relative intensity of diffused light is greater in deeper layer than in shallower. According to his measuring, the diffusion-ratio of under water illumination, which means the ratio between the intensities of illumination on the upward and downward surfaces of horizontal plane, is constant at any depth in homogeneous water. In this connection, Spooner (1933) made some interesting experiments and concluded that the copepods are attracted to the coming light rays, but not to the area where the diffused light is more intensive.

Even though the animals in the deeper layer can discern the difference of intensities between diffuse light from above and from below, phototropic movement will not occur, but the geotropic reaction produced under these circumstances may force the animals to move toward above or below. Thus, the phototropism may control the vertical movement of animals only in the upper layers, but in a great depth the geotropism of animals may be of great importance for controlling the vertical movement instead of phototropism. The geotropism is said to be reversed when the light intensity is changed as well as by the change of temperature as shown experimentally by various investigators, such as Harper (1907), Esterly (1907, 1912, 1919), McGinnis (1911), Dice (1914), Fox (1925), Kikuchi (1938) and so forth. According to the experiment made by Kikuchi (1938), *Acanthodiaptomus yamanacensis* varies its geotropic sign when brought suddenly into diffuse light from darkness or inversely into darkness from diffuse light, but the animals soon become indifferent to the gravity. Foxon (1940) experimented on mysids, finding that dark-adapted animals display negative geotropism, but when a light stimulus is given the sign of their geotropism is reversed.

The geotropic reaction in diffuse light is differently manifested by species as shown by experiment in the present work, and further, the grade of geotropism, positive or negative, in diffuse light is not the same with all species. This difference has relation with the differnce of vertical distribution in the lake. The species having intensive negative geotropism in diffuse light is distributed in the shallower depths than the species which is weakly negative geotrotic in diffuse light. In shallower depths the phototropic reaction also acts in determining the vertical distribution in combination with the geotropism in diffuse light.

However, there is often discrepancy between the results of laboratory experiments on the tropism of animals and the observation of their vertical distribution in nature. Ewald (1910) suggested that sensibility of animals should be higher in nature than is expressed under the circumstances of the laboratory experiments. One can only infer how the behaviour of animals in a glass vessel is related to the movement in nature (Esterly, 1917c). The present experiments show that *Scapholeberis mucronata*, *Bosmina coregoni*, *Acanthodiaptomus yamanacensis* and *Daphnia longispina* subsp. *hyalina* move toward the intensive light even toward the bright sun light. Neverthless, their maximum population is never found at the surface layer of the lake, except in the case of *Scapholeberis*. Kikuchi (1938) also learned by experiment that *Acanthodiaptomus* is found frequently at the position in which the light is most intense, while the phototropism of *Daphnia longispina* varies with the degree of intensity of light. The results obtained by the present experiments might have been much influenced by the effect of artificial environment. All of the species showed higher resistance to the strong light in glass tube than they are in nature.

The vertical distribution in the lake at night may be explained as a reflection of the geotropic behaviour in the glass tube laid in darkness. *Acanthodiaptomus* and *Daphnia* which are nearly neutral geotropic in darkness are distributed without making any particular crowding either in the upper layer or in the lower in the lake at night. *Scapholeberis* is strongly negative geotropic in darkness, and so it is concentrated in the upper water of

the lake at night.

It has been found that the migratory behaviour differs not only with the species, but also with the developmental stage or sex within a species. Nicholls (1933) studied on *Calanus finmarchicus* of Clyde Sea area and reported that the copepodids in stage V do not migrate vertically, while copepodids in stage IV evidently migrate as well as adult females. In the water off Liverpool, Nova Scotia, Gardiner (1933, 1934) found that young *Calanus finmarchicus* dwell in shallower depths than adults do. This is also the case of *Metridia lucens* in the Gulf of Maine (Clarke, 1934a). In the fresh water Lake Kizaki, Kikuchi (1937) learned that the adult males of *Acanthodiaptomus yamanacensis* frequent deeper strata than copepodids do, and the adult females occur deeper than the adult males. Kikuchi, Enokida and Tateno (1942) also noted that the females and males of *Cyclops strenuus* inhabit similar layers, while copepodids are distributed in shallow layers in Lake Biwa; this is also the case of *Eudiaptomus japonicus*. In general the young forms are distributed in shallower layers as compared with adults. In the present observation at Lake Shikotsu it is proved that young *Acanthodiaptomus* go down in August in largest number than in June, as they developed into the later stage in August. The present observations indicate that the adult males of *Acanthodiaptomus* are sensitive to the light condition to a high degree. When the sun is covered with clouds, the males instantly change their vertical distribution. The movement of the females is not so keenly influenced by the change of light condition as is that of the males.

Temperature, dissolved gases and other conditions sometimes affect the vertical distribution of certain plankton. Clarke (1933) mentioned that *Centropages typicus* is distributed above the thermocline (10-20 metres), while *Metridia lucens* is found below it in the Gulf of Maine. The observations in Ishikari Bay (Motoda and Anraku, 1951) and in Funka Bay (Motoda and Anraku, 1952) indicate that such cold water species as *Metridia lucens* and *Pseudocalanus elongatus* are distributed in the water of low temperature below the thermocline. Hansen (1951), investigating in Oslofjord, stated about importance of discontinuity layer (9-11 metres) as limiting factor in the vertical distribution and migrations of the zooplankton. The laboratory experiment by Esterly (1919) shows that *Sagitta bipunctata* does not descend to the lower part of a cylinder filled with sea water chilled as low as 10°C. According to Kikuchi (1930, 1937), *Daphnia longispina* does not appear at the surface even on a dark night when the temperature of the water in the epilimnion exceeds 22°C in Lake Kizaki, vertical migration taking place within the hypolimnion. However, the same species is distributed in the epilimnion in winter season when the water temperature of the surface is low. On account of the same condition, this species was collected by Ueno (1933) in the cold water of the surface in the lakes of Hokkaido during daytime in summer. The work done by Takayasu and Kondo (1936a, 1936b) indicates that *Daphnia longispina* also occurs in the surface water of Lakes Panke and Penke in Hokkaido during daytime in July when the temperature of the surface water is about 20-22°C. However, they (1934a) reported that the majority of this species are found below 10 metres at

Lake Mashu in late August when the temperature of the surface water is 14.5-18.5°C. They (1934b) found abundant individuals of this species in 10 20 metre layers at Lake Toya in October at which time the surface temperature was 16.3 18.2°C. Thus, the above data dealing with the vertical distribution of this species in relation to the water temperature are somewhat complicated. In the present investigation, the cold water form of daphnid, *Daphnia longispina* subsp. *hyalina*, is comparatively scanty above 5 metres at Lake Shikotsu in summer. This is probably due to the high temperature which is 20°C at the surface. On the contrary, another subspecies, *Daphnia longispina* subsp. *longispina*, adapted to warm water in Lake Tsugarujuni, is distributed frequently above 5 metres, especially in dark night.

Acanthodiaptomus yamanacensis (=*Diaptomus pacificus*) has often been collected by several investigators from the surface water in the lakes of Hokkaido in summer season. Takayasu, Igarashi and Sawa (=kondo) (1930) found it in the surface water at Lake Akan; Takayasu and Sawa (1933) at Lake Shikaribetsu; Takayasu and kondo (1936a, 1936b) at Lakes Panke and Penke. However, Hada (1937) reported that this species occurs only below 5 metres at Lake Panke in winter. It is noticed that this species does not migrate diurnally in Lake Akan, remaining always in the surface water (Takayasu, Igarashi and Sawa, 1930). *Acanthodiaptomus* at Lake Tsugarujuni in the present investigation is always distributed in the maximum number at 5 metre layer. Even in dark night the number in the surface layer, in which the temperature is about 25°C, is not so large as in the corresponding level at Lake Shikotsu.

Bosmina longirostris at Lake Tsugarujuni is abundantly found in the warm epilimnion and displays diurnal migration within this range. However, Kikuchi, Enokida and Tateno (1942) reported that this species in Lake Biwa occurs below the thermocline in summer.

The lack of dissolved oxygen together with the existence of hydrogen sulphide in the deep layers of lake water usually excludes the inhabitation of the plankton animals. At Lake Suigetsu (Kikuchi, 1931) and Lake Harutori (Hada, 1938) such examples have been reported. In the present investigation the oxygen content of the water at Lake Tsugarujuni was 5.94 cc/l at the surface, while only 2.52 cc/l at 12 metre depth. The plankton animals would suffer from the change in oxygen content, as it becomes less than a half of that of the surface, when they descend to 12.5 metres. However, the vertical migration of plankton seems to be not checked by the diminution of oxygen content in such degree.

The verticcal distribution of plankton is said to be influenced in some cases by the food organisms which are abundantly distributed in some particular depth. It has been reported that there occurs sometimes a concentration of protozoans in the thermocline, and that crustaceans and rotifers are crowded there to devour them. Hardy (1936a, 1936b) after investigating in the Antarctic Ocean on board the "Discovery" stated that zooplankton migrates up to the surface water to feed upon the phytoplankton during night, but when there is abundant phytoplankton, the zooplankton soon migrates down

again to a great depth, owing to the effect of "animal exclusion" of phytoplankton. According to Bainbridge's (1949) experiment, *Neomysis vulgaris* moves actively into one end of glass tube where the diatoms are concentrated, but it does not move into filtered water, nor into green coloured water, nor into the diatom concentration in the dark. The behaviour seems to be different from that manifested in nature, because the plankton migrates to the upper water to feed on diatoms at dark night in the sea. *Acanthodiaptomus* in the present observations, especially young forms, which are thought to be most voracious, do not occur abundantly in the surface water even in dark night at Lake Tsugarujuni. This will have some relation to the vigorous propagation of phytoplankton in this lake. The animal plankton might feed sufficiently under the surface and there is no need to come to the surface.

IX. Conclusion

Two lakes, Lake Shikotsu and Lake Koikuchinoike of the Tsugarujuni Lake Group, the sites of the present investigation, differ greatly in transparency, which is measured above 20 metres in the former, and only about 5-6 metres in the latter. In both lakes, most of the plankton crustaceans display diurnal movement, descending during the daylight and ascending at dark night. Only *Scapholeberis mucronata* remains in the upper layer in daytime as well as at night. All species are distributed in shallower layers at Lake Tsugarujuni than at Lake Shikotsu, evidently due to the less intensity of underwater light in the former lake as compared with the latter. The vertical distribution of various species in fine weather in daytime is different from the distribution in cloudy weather at Lake Shikotsu, the plankton animals being more remarkably stratified in fine weather. The vertical distribution of adult *Acanthodiaptomus* at Lake Shikotsu is at shallower levels in autumn than in summer, and the duration of appearance in the shallow water at night becomes long in autumn. These facts affirm the intimate relation between the vertical movement of plankton and the change of light intensity. Futhermore, certain species show an evident tendency to avoid the bright light of the full moon, decreasing in number at the surface water.

The type of vertical distribution of plankton animals varies not only with the species but also with sex and stages in development. The males of *Acanthodiaptomus* are more sensitive to light than the females, their movement up or down quickly reflecting the change of light condition. The vertical distribution of the copepodids of *Acanthodiaptomus* in the morning (6:00 a. m.) and in the evening (6:00 p. m.) in August is nearly simlar to that observed at corresponding times in June in spite of the fact that solar irradiation at these hours is far weaker in August than in June. Moreover, they are distributed in shallower layers in daytime in June than they are in August. Thus the copepodids in advanced developmental stage in August may become highly sensitive to the light and tend to avoid the light, descending to a certain depth.

The grade of positive phototropic reaction and negative or positive geotropic reaction in diffuse light of various species as observed by the laboratory experiments corresponds to the diversity of vertical distribution in the lake in daytime. The form exhibiting strong positive phototropism and strong negative geotropism in diffuse light is distributed in upper layers in the lake, and conversely the form exhibiting weak positive phototropism and weak negative geotropism or positive geotropism in diffuse light prefers the lower layers.

The vertical distribution in the dark night is related to the geotropism in darkness as experiments show. The neutral geotropism in darkness forces the animals to be scattered from the upper layer to the lower at night, resulting in nearly uniform vertical distribution, but the negative geotropic reaction in darkness makes the animals to ascend to the upper layers at night.

There is an evidence that the males of *Acanthodiaptomus* are remarkably concentrated in upper water in the evening twilight and following dark night for certain hours at Lake Shikotsu, while they do not display such a particular ascending at dawn. The animals have been exposed to the daylight for several hours in daytime may exhibit abrupt upward movement when the light stimulation is ended in the evening twilight.

Only a few *Daphnia longispina* subsp. *hyalina* occur above the 5 metre depth even in dark night at Lake Shikotsu in summer, when the water temperature in the epilimnion is above 20°C. The high temperature in the epilimnion works to exclude certain species. This subspecies is found abundantly at the surface in June, when the temperature of the surface water remains at about 15°C. Differently from the above subspecies, another subspecies "*longispina*" at Lake Tsugarujuni, which is regarded as a form preferring warm water, moves up in large numbers to the surface during night, in spite of the temperature of the surface being as high as 25°C. On the other hand, most of *Bosmina longirostris* at Lake Tsugarujuni do not descend below 5 metres, probably owing to the existence of cold water there.

The number of *Acanthodiaptomus*, particularly the copepodids, is decreased in the surface water even at night at Lake Tsugarujuni. This may be related to the plentiful food in this lake and partly to the high temperature of the surface water. When there is plenty of food in a certain depth, the animals can get nourishment without ascending to the surface.

In conclusion, it would be regarded that the plankton crustaceans observed at Lake Shikotsu and Lake Tsugarujuni in the present investigation generally display the diurnal vertical movement with the change of light intensity. Of course, the behaviour differs in detail according not only to the species but also to the sex and developmental stages. As the grade of phototropic and geotropic reactions under various external conditions varies with species and forms, and some species avoid high or low temperatures, while others are indifferent to changes of temperature, the behaviour in diurnal movement of each species is manifested in different ways.

X. General Summary

(1) Diurnal vertical migration of plankton crustaceans at Lake Shikotsu in Hokkaido and at Koikuchinoike of the Tsugarujuni Lake Group in Aomori Prefecture was observed. The lake water of the former is very transparent, while that of the latter is considerably turbid.

(2) Together with the field observations on vertical distribution, some laboratory experiments on the photo- and geotropism of plankton crustaceans were carried out in this relation.

(3) In summer at Lake Shikotsu when the weather is fine, the females of *Acanthodiaptomus yamanacensis* which are distributed nearly uniformly through vertical range from the surface to about 20 metres during night, disappear from the surface at dawn about 5:00 a. m., becoming absent above the 5 metre level at 10:00 a. m. The number of animals is very scanty above 10 metres, a majority of them being distributed in 10-20 metres at noon. Some appear again in the 5 metre layer at 1:00 p. m. and the maximum layer ascends to 5 metre level at evening dusk at 7:00 p. m. The crowding in shallow layer at evening dusk is very remarkable, but this is not observed at dawn. After 9:00 p. m. nearly uniform vertical distribution is shown again. Under heavy clouds the maximum layer in daytime is always shallower than in fine weather. In autumn the animals are distributed in the level shallower than in summer, and stay at the surface at night much longer. At Lake Tsugarujuni the females of *Acanthodiaptomus* also show diurnal movement, though in small degree. The number of animals is small above 2.5 metres in this lake. The animals may feed on the plentiful food under the surface and so they need not come to the surface. They appear at 2.5 metre level and the maximum number is found at 5 metres in sunny midday, though they are absent at the surface.

(4) The males of *Acanthodiaptomus yamanacensis* at Lake Shikotsu show more distinct stratification than the females do both in daylight and dark night. Upward migration in the evening dusk is most remarkable in the males. They do not show any particular crowding in the shallow layers at dawn. The tendency of the males to ascend in cloudy weather and to descend under the bright moon is manifested more distinctly than that of the females. The distribution of the males at Lake Tsugarujuni is shallower than at Lake Shikotsu as is true of the females. Thus, it may be stated that the males are more sensitive to the light than the females, displaying a diurnal migration more closely related with the change of intensity of light.

(5) The copepodids of *Acanthodiaptomus yamanacensis* display the same diurnal migration at Lake Shikotsu as the adults, but the number of individuals occurring in shallow level in daytime is large, indicating that the copepodids are less sensitive to the light than the adults. They are distributed nearly uniformly at night. The vertical

distribution at 6:00 a. m. and 6:00 p. m. in both June and August is almost the same, despite the longer duration of daylight in the former month. Moreover, the layers in which the animals crowd in daytime is shallower in June than in August. These facts force one to assume that the animals become sensitive to the light as they grow to more advanced stage. The distribution of copepodids at Lake Tsugarujuni shows that they scarcely inhabit the surface water even at night. As mentioned in the case of adults, the scarcity of young individuals in the surface water may be related to the plentiful supply of food in the water below the surface.

(6) *Daphnia longispina* subsp. *hyalina* at Lake Shikotsu also shows diurnal movement. The animals are abundantly distributed below 10 metre layer under the bright sun in June, August and October. They come to the surface after 6:00 p. m. and descend at 6:00-8:00 a. m. The maximum number is found in 0-5 metre layers at night in June, while in August it is at 15 metres. The temperature, higher than 20°C, in the epilimnion in summer checks the upward migration beyond the thermocline.

(7) *Daphnia longispina* subsp. *longispina* at Lake Tsugarujuni is found in large numbers below 5 metres, some appearing at 2.5 metres, with the maximum at 7.5 metres, in a bright midday. In dark night the number of animals at the surface increases, where the temperature is as high as about 25°C, and the maximum layer is at 5 metres. Actual vertical migration is seen occurring above the thermocline.

(8) *Scapholeberis mucronata* at Lake Shikotsu is distributed in upper layers, appearing abundantly at the surface, in daytime and it is also found at the surface at night. According to the laboratory experiment, this species is strongly negative geotropic in darkness (cf. 15).

(9) *Bosmina coregoni* at Lake Shikotsu shows the maximum distribution in 20-25 metres in a fine weather in autumn. However, in a cloudy weather the number of animals in the upper layers increases, though the maximum layer does not vary. Scantiness of the animals in the shallow layers has no relation to the temperature, as the temperature of the epilimnion is not high, about 14°C, at Lake Shikotsu in autumn, but for this the positive geotropism in diffuse light may be responsible (cf. 14).

(10) *Bosmina longirostris* at Lake Tsugarujuni shows maximum abundance in 2.5-5 metres at noon in fine weather. Active vertical migration takes place within the warm epilimnion.

(11) *Cyclops strenuus* at Lake Tsugarujuni displays diurnal movement passing through the thermocline. The maximum layer descends below 12.5 metres in daytime. The distribution at night is nearly uniform, though the number of animals at 9.5 metres is comparatively large.

(12) The maximum number of *Eucyclops prasinus* is found at 5 metres in daytime, while it is at 2.5 or 5 metres at night in Lake Tsugarujuni.

(13) Laboratory experiments revealed that the grade of positive phototropic reaction at ordinary temperature is in the order as follows: *Scapholeberis mucronata*; *Bosmina*

coregoni; *Acanthodiaptomus yamanacensis*; *Daphnia longispina* subsp. *hyalina*.

(14) The females of *Acanthodiaptomus yamanacensis* are negative geotropic in diffuse light at ordinary temperature, and the males are strongly negative, while *Daphnia longispina* subsp. *hyalina* is strongly positive, and *Bosmina coregoni* is also positive. *Scapholeberis mucronata* is as strongly negative as the male *Acanthodiaptomus*.

(15) In darkness at ordinary temperature, geotropism of both the females and males of *Acanthodiaptomus yamanacensis* is neutral. *Daphnia longispina* subsp. *hyalina* also does not react particularly to gravity. *Scapholeberis mucronata* is strongly negative and *Bosmina coregoni* is also negative.

(16) The diversity of vertical distribution of various plankton crustaceans at Lake Shikotsu in daytime is considered to be a reflection of their diversity in degree of phototropic reaction and geotropic reaction in diffuse light as observed in the laboratory experiments.

(17) Similarly the geotropic reaction in darkness is reflected in the vertical distribution in the lake on a dark night.

(18) The plankton crustaceans placed in the experimental glass tube behave somewhat differently from the way they do in nature, generally becoming less sensitive to the stimulation of the sun light.

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ADDENDUM

According to the recent studies of Ito (1953), all the *Acanthodiaptomus* in Japanese lakes should be regarded as *Acanthodiaptomus pacificus* (Burckhardt). (Ito, T., 1953. Studies on the morphological variation in natural populations of Calanoida-Copepoda of Japanese inland waters. Jour. Fac. Fish., Pref. Univ. Mie, Vol. 1, No. 3, pp. 273-400, in Japanese)

Table 1. Vertical distribution of plankton crustaceans at 10:30 a. m. on August 20th, 1942, under bright sun in the deep water of Lake Shikotsu (Observation 1). Numbers of plankton denote the individual numbers in a towing of net for 100 metres.

Depth (m)	*Acanthodiaptomus*	*Daphnia*	*Scapholeberis*
0	150	0	9160
10	85400	1	2050
30	10820	85	43
50	1310	1	19
80	100	2	13

Table 2. Vertical distribution of plankton crustaceans in daytime under bright sun on August 15th, 1943, in the deep water of Lake Shikotsu (observation 2). Numbers of plankton denote the individual numbers in a towing of net for 100 metres.

Hour	Depth (m)	*Acanthodiaptomus* ♀	*Acanthodiaptomus* ♂	*Acanthodiaptomus* copepodid	*Daphnia*	*Scapholeberis*
9:00 a. m. —	0	2	9	5	0	550
	5	200	14	1970	8	790
	10	76	36	2420	100	4
	15	440	2290	1030	190	16
	20	330	580	430	420	10
9:40 a. m. —	25	410	84	140	570	40
	30	780	48	140	350	100
	35	Failed	Failed	Failed	Failed	Failed
	40	520	24	110	84	56
	45	470	22	68	56	12
10:10 a. m. —	50	300	32	32	46	6
	55	94	1	44	13	47
	60	97	2	53	18	42
	65	59	9	44	13	26
	70	32	8	48	18	5
10:50 a. m. —	75	49	4	19	15	1
	80	62	5	8	3	4
	85	34	2	14	17	1
	90	28	3	33	21	7
	95	48	2	43	21	26
11:30 a. m. —	0	1	2	27	0	1340
	5	8	12	2010	8	230
	10	180	120	6130	16	210
	15	820	3790	1510	310	8
	20	1010	1390	780	3020	0

Table 3. Vertical distribution of plankton crustaceans in daytime in October, 1946, in the deep water of Lake Shikotsu (Observation 3). Numbers of plankton denote the individual numbers in a towing of net for 100 metres

(A) Under heavy clouds on Oct. 18th.

Hour	Depth (m)	*Acanthodiaptomus* ♀	*Acanthodiaptomus* ♂	*Daphnia*	*Scapholeberis*	*Bosmina*
12:20 — 12:30 p. m.	0	340	1060	320	850	80
	5	830	4920	1690	44	92
	10	1150	7650	1570	32	270
	15	1570	10690	1490	30	540
	20	1470	9310	2940	0	2430
	25	2880	9760	2430	0	8000
12:45 — 12:55 p. m.	25	2500	8060	4030	0	3780
	30	Failed	Failed	Failed	Failed	Failed
	35	Failed	Failed	Failed	Failed	Failed
	40	6140	2370	3780	0	64
	45	1660	1130	1470	0	48
	50	980	550	690	0	52

(B) Under bright sun on Oct. 19th.

Hour	Depth (m)	*Acanthodiaptomus* ♀	*Acanthodiaptomus* ♂	*Daphnia*	*Scapholeberis*	*Bosmina*
11:50 a. m. — 12:00 m.	0	66	170	9	1060	25
	5	28	210	26	750	52
	10	140	2210	390	23	24
	15	1730	18690	990	15	190
	20	4220	22210	4290	0	9660
	25	3140	5760	5030	0	8830
11:20 — 11:30 a. m.	25	2500	6080	3780	0	9090
	30	2240	1980	2300	0	1560
	35	830	1440	1580	0	240
	40	470	1350	1290	0	270
	45	520	1210	920	0	430
	50	470	1430	710	0	300

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